VOLUME XLVII NUMBER 2

BOTANICAL GAZETTE

FEBRUARY 1909

RELATION OF SOIL AND VEGETATION ON SANDY SEA SHORES

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(WITH TWELVE FIGURES)

The studies on which the present paper is based were carried on during a number of years on a variety of sandy sea shores on the Baltic coasts, in Denmark, Holland, Scotland, and France, on the Mediterranean shores, along the coasts of Australia and New Zealand, in Hawaii, California, Mexico, and Central America.

In this paper I propose to give some of the observations made by myself regarding the conditions for plant life on coastal sand formations, and also to compare these investigations with the accumulated results from studies on this subject obtained by others.

Although considerable attention has been given to some of the most important points, I have as yet not been able to study in detail others, equally weighty; and in trying to interpret several of the phenomena of the distribution of sand vegetation I have found myself confronted with many problems, for the solution of which there is but little definite evidence at hand.

In discussing the factors that influence plant life, I have found it convenient to classify them into the following groups: atmospheric, hydrodynamic, edaphic, topographic, and historical factors.

To atmospheric factors all those are here referred, which directly influence the vegetation through the air. The atmospheric temperature, the light conditions, the variations in air moisture, the movements in the atmosphere, and the electricity are the principal factors of this kind. As hydrodynamic factors I understand all those connected with the water content of the substratum, and edaphic factors are

those relating to the chemical and physical quality of the soil. I call topographic those factors which have reference to the external features of the ground, and they affect indirectly more or less the factors belonging to previous groups. Historical factors are those which in the course of time exert an influence on the topography and thus indirectly on the plant covering.

Another series of factors analogous to the physical factors influencing plant life are the biotic. They are either zoobiotic or phytobiotic. Of the former especially the influence of man has to be recognized in connection with the study of vegetation on coastal sands. The phytobiotic factors are those caused by the plants themselves, and the mutual relationship of sand plants will be discussed in another paper.

Atmospheric factors

It is impossible to determine the relative importance of different factors influencing plant life, or to give one of these factors precedence in rank before another, because this depends in different cases on different conditions. It may be said, however, that the whole group of atmospheric factors is the most important, especially because of their influence on the transpiration of the plants. Sand vegetation is particularly affected by: (1) the large amount of heat absorbed by the sandy ground and reflected from its surface; (2) the intensity of illumination, both direct on the open, unprotected formation, and reflected from the white sand; (3) the exposure to winds, which constantly change the atmosphere.

TEMPERATURE.—If we compare in a general way the temperature conditions in a few of the localities under consideration, we find that there is no significant difference in results as regards development of sand formations or their vegetation in cold and warm countries. On the dunes along the Gulf of Finland, where the vegetation is in a dormant state for at least three months of the year, the sand drifts best during winter, when the grains are covered with a thin surface of ice, and are smooth. The friction is less and they are able to move slowly forward. The herbaceous vegetation is absent at this time, and the deciduous shrubs are without leaves. There is consequently nothing to arrest the movement of the sand.

On the Queensland coast, with a semitropical climate, the vegeta-

tion period extends over the whole year, but the sand drifts here much better during the summer, because winter is the rainy season, and when wet the coherence of the sand is greater. Plants like Ammophila, Cakile, Salsola, and Atriplex, of which the parts above ground die every winter on the Baltic coasts, grow all the year round on the shores of Australia, and there is no difference, external or internal, in structure. *Convolvulus soldanella* on the coast of Holland does not differ from the same species on the shores of tropical countries, where it is common (*fig. 10*).

Dunes are formed in warm countries more generally than in cold because of the longer periods of drought, which favor the drifting of the sand. We refer to the enormous areas of sand formations in Africa, both on the coasts and in the interior, in the deserts of Asia, on the coasts of India and Australia, in the interior of the latter continent, on numerous tropical coasts as Java, Hawaii, etc. The dunes which occur in really cold countries, as in certain parts of the United States and northern Europe, are insignificant in comparison with the former.

It would be of considerable interest to have correct data of temperature conditions from the various localities where the author has made his studies of the coastal sands. The field-work on which this paper is based, however, has been conducted for comparatively short periods at each place, and the temperature observations made do not offer, therefore, any reliable basis for comparisons. Official data, obtained from meteorological stations on the coasts, are also unsatisfactory for our special purpose, because the instruments usually are kept close to buildings, away from vegetation, in more or less sheltered positions, and because of these facts the observations cannot serve for any definite conclusions as to the real temperature conditions under which the vegetation has developed. It is not necessary to burden these pages with computations of any general data of the kind referred to. The author has compared a great number of temperature statistics from different coasts, but he has entirely failed to find any apparent rules applicable to the development in general of sand vegetation in different climates. This negative result is not due to absence of such laws, which certainly must exist. It merely shows that our knowledge is deficient and the present method of taking temperatures at meteoro-

logical stations is entirely inapplicable to the subject under consideration.

For ecological purposes temperature observations in the field have to be made very carefully if we are to draw from them any conclusions of value as to the influence of heat on the vegetation. And further, they have to be extended over a long period of years before we are justified in advancing any general laws of temperature influence on distribution of plants.

Let us here draw attention to the opinion held on this question by the greatest authority on ecology, Professor WARMING. In his renowned handbook on ecological phytogeography (**14**) he says on page 22, speaking of the many attempts to determine the sum-totals of temperature in relation to geographical distribution, that these investigations need in a very high degree to be supported by really scientific experimental determinations of the cardinal temperatures for the phenomena of different species. And even the results of such observations would hardly be sufficient for the solution of the very difficult and complicated questions of the importance of heat conditions for distribution of species and phenological phenomena, as other factors, perhaps, to some extent can replace a higher temperature.

One feature of the heat conditions on coastal sands is apparent. That is the great fluctuation of diurnal temperatures. On account of the low specific heat of sandy soil, the surface layers are rapidly heated by the sun in daytime and as quickly cooled by night. These variations of temperature are conducted by radiation to the lower strata of the atmosphere, or those in direct touch with the plants, which consequently are greatly affected by such changes.

Of some occasional observations by the writer on the diurnal range of temperature on sand dunes the following may be mentioned as examples of the great divergence between temperature extremes in such localities.

Observation 64.—Dunes at Hangö, Finland, September 10, 1897. Maximum temperature in the shade (thermometer from unknown maker) 28°.8 C., between 6 A. M. and 6 P. M. Minimum (thermometer from WALLMANN in Stockholm) 2°.6 between 6 P. M. and 6 A. M. Range 25°.6. The instruments were placed on an open sand surface 25^{cm} above the ground, and were shaded by white canvas, 2^{m} high. Ordinary thermometer readings in the shade were taken every hour in the daytime, giving the following results:

6 A. M. 8°.5 C.	10 A. M. 14° C.	2 P. M. 23°.6 C.
7 A. M. 9.2	11 A. M. 17	3 P. M. 27.2
8 A. M. 9.8	12 M. 19.4	4 P. M. 27.5
9 A. M. 11.4	1 P. M. 20.6	5 P. M. 22.4
		6 P. M. 15.9

This place of observation was on an open spot, unprotected from the winds. About 60^{m} inland between the pines, and sheltered from winds, the thermometer gave 7°.4 C. at 6 A. M., 9°.2 C. at 9 A. M., 16°.6 C. at noon, 28° C. at 3 P. M., 16°.2 C. at 6 P. M. This shows that the temperature was slower to rise in the morning and forenoon, but once high it was also slower to decrease, when the energy of the solar rays was diminishing toward evening.

Observation 576.—Dunes at North Beach, near Perth, Western Australia, September 12, 1902. Maximum in the shade 31°.1 C. (8 A. M.–6 P. M.). Minimum 6°.8 C. (6 P. M.–8 A. M.). Range 24°.3. The instruments, from NEGRETTI & ZAMBRA in London, were elevated 30^{cm} above ground and shaded by a white canvas tent with open sides. The hourly variation was the following:

8 A. M. 7°.9 C.	12 M. 23°.6 C.	4 P. M. 19°.5 C.
9 A. M. 11.2	1 P. M. 29.4	5 P. M. 16.3
10 A. M. 15.6	2 P. M. 30.7	6 P. M. 9.6
11 A. M. 18.6	3 P. M. 20.3	

These data show, as in the previous observation, that the temperature rose steadily until about 2 P. M., although the rise is so much more rapid in these latitudes on account of the greater energy of the sun. In this case, however, over 10° in a single hour, and nearly 10° more between 4 and 6 P. M.

On the coast of Western Australia a sea breeze always sets in about noon, according to COOKE (**4**), the temperature then begins to fall until evening, and the nights are generally cool the whole year round.

The influence on vegetation of such a wide range of temperatures must necessarily be of considerable importance. Although these air temperatures have been largely affected by radiation, the direct radiant heat of the sun is still more important. Actinometric methods of registering intensity of solar radiation are, as yet, very unsatisfactory. Almost the only instrument available for field observations is the so-called black-bulb thermometer *in vacuo*. The rather casual observations of this kind made by the writer will be referred to in another place in connection with some transpiration phenomena. It may suffice, however, to say here that these occasionally taken measurements, in spite of their discontinuity, have convinced the writer that the surest and most effective way of attacking the problems of heat influence on vegetation is to pursue investigations on the lines of actinometric records. Neither the mean temperature of the air nor the sum-total of atmospheric temperature is of such importance

to vegetation as the amount of direct solar radiation and radiation of heat from the ground. The value of the former factor in climatology has long been recognized by meteorologists.

We must never lose sight of the fact, however, that it is not one factor alone that determines the development and distribution of the vegetation, but a resultant of the many different conditions to which the plants are subjected. This has been duly emphasized by WARMING (**14**).

LIGHT.—In the closest relation to atmospheric temperature, and especially to radiation of heat, is the factor of light. The intensity of illumination is remarkably large on the open sand formations of the coast, and this circumstance is noticeable in the many protective adaptations of plant structures against the influence of light. There are as yet no reliable means of ascertaining the intensity of the light, and we have consequently no basis for comparisons on this subject. The strong insolation on the white surface of the sand favors a greater variation of temperatures than on other formations of the coast. The radiation is, however, generally less on the coast than in localities far away from the sea because the larger quantity of aqueous vapor in the atmosphere in the former place tends to check this terrestrial radiation.

HYDROMETEORIC CONDITIONS.—This term has here been used to distinguish the factors of atmospheric humidity from those of the water content of the soil or the substratum from which the plants take their supply. On coastal sands it is perhaps more apparent than on other formations that there is some difference in influence and effect on vegetation of the moisture contained in the air and of the water in the soil. It is, however, always extremely difficult to decide to what extent certain adaptations are due to one factor more than to another, especially when we do not possess detailed observations.

AIR MOISTURE AND EVAPORATION CAPACITY.—The supply of atmospheric moisture is to a great extent obtained from the ocean, and it follows that on the coast the amount of humidity must be much greater than farther inland. This is in fact an everyday observation.

We do not know for certain to what extent the plant is able to condense water vapor and absorb atmospheric humidity, but we do know that moisture in the air greatly lessens transpiration, and, other factors being equal, transpiration ought therefore to be less on sea shores than

inland. Now it is not the absolute humidity that determines the amount of evaporation, but the saturation deficit or the amount of water which the atmosphere at a certain temperature is able to absorb (WARMING). In the continental interiors the evaporating power of the climate is very great during summer, and on account of the cold quite inconsiderable during winter (HANN **7**). If we compare the habits of certain plants which occur both in the interior deserts, and on coastal sands we shall find them instructive. For instance *Mesembryanthemum aequilaterale* has the same appearance when growing on the beach or in the immediate neighborhood thereof, as when occurring on the interior sands of Australia, many hundreds of miles from the coast. But when found at a certain distance, 0.5^{km} or so, from the beach, *outside the influence of the spray from the sea, and sheltered from the full force of the ocean,* it grows higher, its leaves are two or three times as long, and its succulence is less marked than in specimens from the beach or from the interior. In the case of the writer's observation, the places of growth were as nearly similar as possible with regard to exposure to the rays of the sun and moisture in the soil. Some notable differences in anatomical characters observed in this connection will be alluded to in another paper. These characters also proved that the devices for protection against excessive transpiration were not so well developed in the specimens which were not exposed to the strong salt-laden winds, although they had the full benefit of the coastal moisture.

If we may be allowed to draw any inferences from this fact, we should conclude that, as a rule, *transpiration is less on coastal than on interior sands.* There are other factors, however, to be taken into consideration, which somewhat equalize the conditions, as the wind and the salinity of the atmospheric moisture.

Everywhere on warm coasts, especially in the neighborhood of the sea, on the beach, we can notice a peculiar sand flora. It is characterized by species which do not occur farther inland, and on the other hand inland plants as a rule do not go down to the beach. The greatest part of this strand flora consists of halophytes or plants growing in salty situations.

It is generally assumed that the conditions in which halophytes thrive are dependent on the amount of salt present in the soil. As

we shall show, when speaking of the edaphic factors, the quantity of salt present in the soil in some of the coast formations is quite inconsiderable, but still the plants exhibit the same characters typical of those which grow where salt occurs in the soil.

We cannot here escape the conclusion that the influence which is exerted on the plants in one case by the salt-water content in the soil, in the other case is brought about by some other cause of similar kind.

Analysis of spray from the sea reveals the presence of a large amount of salt, usually even more than in the sea water, because water is evaporating from the drops of spray and the fine particles of moisture near the ocean. This salinity of the spray is greater at a high temperature, as the evaporation is then more intense, and it is common to find on hot days, with sea wind carrying moisture landward, that salt is deposited in form of crystals on the plants and on other objects, as well as on the ground.

A few analyses will be given to illustrate this large quantity of salt in the atmosphere on the sea coast. In all instances when samples of spray were secured, the method was as follows. Pieces of muslin, thoroughly examined and found free from salts, were dried and kept in tight-closed jars until exposed at the place were the sample was to be taken. The muslin was then exposed to the sea spray; the temperature and time of exposure were registered, the muslin bottled, and later examined in the laboratory. At the same time samples of the sea water were secured for chemical analysis. The following results were obtained from four observations:

I. Nagu, Högsar, Finland, August 22, 1897. Atmospheric temperature 19°.5 C. Sky clear. Velocity of wind about 7^m a second. Muslin exposed for $1^h\ 15^m$, at a distance of 9^m from the water. Salinity of spray sample 0.673 per cent., of sea water 0.662 by areometric measurement, and 0.632 per cent. by chemical analysis. Temperature of water 15°.0 C. As is the case in this observation the areometric value of salinity is always somewhat higher than that obtained by analysis.

II. Hangö Tulludd, Finland, September 9, 1897. Atmospheric temperature 21°.2 C. Sky partly overcast. Velocity of offshore wind about 10^m a second. Muslin exposed on the beach, 5^m from water, for 2^h. Salinity of spray sample 0.625 per cent., of sea water 0.607. Water temperature 13°.6 C.

III. North Beach, near Perth, Western Australia, September 16, 1902. Atmospheric temperature 24°.6 C. Sky clear. Velocity of wind, measured with anemometer (of Crova type, from NEGRETTI & ZAMBRA, London) averaging 12.3^m a second during time of observation. Muslin exposed on the beach, 8^m from the water, for $4^h\ 15^m$. Salinity of spray 4.68 per cent., of sea water 3.24 per cent. Temperature at the surface 10°.6 C.

IV. Beach at Pialba, Queensland, on the eastern coast of Australia, June 17, 1901. Atmospheric temperature 16° C. Sky clear. Velocity of wind about 6^m a second. Muslin exposed 5^m from the water. A heavy surf was rolling at the time, but as the water is shallow far out from shore, and sheltered by clumps of mangrove, the breakers did not strike the shore with any force. The sample showed a salt content of 4.1 per cent. Salinity of ocean water 2.91 per cent., and temperature 9°.4 C.

Although the presence of sodium and chlorine, as common salt, can be shown in many inland plants, a larger percentage of these salts is found in the ash of strand and marine plants than in that of the former type.

Whether these salts are absolutely essential for any plant we do not know for certain. If that is the case, the amount of salt needed is very small, as has been shown by several investigators. Even for many marine algae only the smallest quantities of salt are necessary, if at all essential.

Inland plants are, however, unfavorably influenced by a percentage of salt which strand plants bear without injury; on the other hand, it has been proved by cultures, that the halophytes can grow without the usual amount of salt contained in the soil or atmosphere of their natural habitat.

An interesting experimental study of strand and other plants with relation to common salt and sea water has been made by COUPIN (**5**). He found that 1.5 per cent. of common salt in soil or in water is poisonous to plants which do not naturally grow on the sea shore. Sea water contains about 2.5 per cent. of common salt, and the soil washed by the sea, as well as the atmosphere near the coast, contains still more than this proportion. We can thus readily understand the sharp line which separates the marine and strand floras from those of the interior. COUPIN attributes the poisonous property of sea water for inland plants mainly to its content of common salt, for the two salts next to this in abundance, magnesium sulfate and magnesium chlorid, are present in quantities which he considers below the toxic proportions. Magnesic sulfate is poisonous at a concentration of 1 per cent., magnesic chlorid at 0.85 per cent., but they occur in sea water only to the extent of 0.75 per cent. and 0.5 per cent. respectively.

The question of the influence of salt on strand plants and of the

absorption by the plant of saline water has been discussed considerably, and several theories have been advanced.

PRECIPITATION is a factor, which on naturally dry soil, such as presented by sand formations, is of considerable importance, not only on account of the quantity of water which in this way is brought to the plants, but also because of its influence in giving coherence to the sand, thus preventing it from shifting, and because of its weathering action on the soil particles.

That precipitation must to a great extent influence the development of vegetation on marine coasts is evident, and it is easily seen that the composition of the plant covering of sand formations varies somewhat in rainy and rainless climates, although the atmospheric humidity on the coast tends to minimize this difference. The latter factor is especially important as the precipitation often is so variable. The absolute amount of rain during the year does not in fact give any correct basis for comparison of the conditions in different localities, as it is far more important for the vegetation how this quantity is distributed over the period in question. On the Baltic shores the number of rainy days of the vegetative season is much greater than, for instance, on the coast of Australia or California. The eastern coast of Australia, at Brisbane, has an average yearly rainfall of 129.5^{cm} while the Åland Islands in the Baltic have only 52.9^{cm}, but the vegetation in the latter region has a much more even supply of moisture during the vegetative season, because the precipitation is distributed over a greater number of days, about 70 of the 160 rainy days of the year falling in the growing season.

Edaphic factors

When SCHIMPER proposed this term (1898) he apparently regarded it as covering all the peculiarities of the ground. It seems to the present writer that it would be more convenient in this connection to distinguish between the soil as such, and the media, water and air, filling the interstitial spaces. This distinction has been made in this paper by separating the factor of soil moisture under the heading *hydrodynamic*, and the factors pertaining to the soil proper as *edaphic*.

The hydrodynamic factors are now generally admitted to be of the very greatest importance for the vegetation and its distribution. I

have treated this subject in another place (**12**). With regard to the edaphic factors, *sensu scriptoris*, a wide difference of opinion has prevailed. While some writers have maintained that the chemical influence of the soil is the most important, others have been in favor of the theory which gives to the physical properties of the soil the largest bearing. Since the physical conditions mainly determine the amount of water, most recent authors upon the subject, among them WARMING, hold that these are of greater consequence.

In discussing the physical conditions of sand formations we will confine ourselves to the question of soil temperatures, and further briefly refer to some measurements of the size of sand grains made by the writer.

SOIL TEMPERATURE.—The heat-absorbing power of sand is low in comparison with other darker-colored soils, but because the radiation is great the vegetation on a surface of sand is subjected to a comparatively high temperature. As the sand is always moist only a little below the surface the heated layer of sand does not reach deep before it meets lower temperature.

The roots always penetrate to this moist layer, and only the upper part of the root is under the influence of the heat of the surface stratum of sand. We find corresponding adaptational protections on the roots of most plants growing in sandy soils.

The transport of heat within the soil is influenced by several factors outside the conductivity from one layer to another. It is impossible, however, in the natural state of the soil to eliminate these factors, the movements of water and air in the soil, the evaporation of water from the warmer and condensation of water vapor in the colder strata. The data here supplied therefore represent the temperature of the soil under conditions such as it presents in the field.

In all observations made by the author ordinary soil thermometers were used, and the temperature was taken at following depths: 2, 5, 10, 20, and 50^{cm}. The bulb of the instrument can easily be placed in loose sand at the desired depth. The number of complete series of observations made on different sand formations reaches 876. Some of these will here be referred to, and in other cases average values will be given.

On the front beach the temperature of the soil is varying more

than on other formations of the sand strand, because of the frequent inundations and subsequent changes in evaporation. It is generally low as compared with that on the higher parts of the beach. Seven measurements taken at Högsar, Nagu, Finnish Archipelago, in June, 1894, averaged 16°.4 at a depth of 2^{cm}. The corresponding data, obtained at varying depths, are shown by Table I.

TABLE I

	2 cm.	5 cm.	10 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness 1–10
1.....	18.3	16.3	17.4	19.6	18.4	12:30 P. M.	1.5	2
2.....	14.9	15.5	16.3	13.8	16.6	2:00 P. M.	0.5	6
3.....	19.6	18.9	18.6	19.8	16.7	11:30 A. M.	4.1	4
4.....	16.5	15.8	15.9	16.5	16.9	2:00 P. M.	0.3	0
5.....	14.2	14.6	15.2	14.4	16.5	1:30 P. M.	2.6	1.5
6.....	13.3	13.6	12.9	14.0	15.6	1:30 P. M.	1.8	2
7.....	16.7	15.4	14.7	16.9	16.5	2:00 P. M.	0.4	1

In all cases except 3 the sand was covered with vegetation, in 5 and 7 with *Glaux maritima*, in 2 with *Erythraea litoralis*, in 1 and 4 with *Argentina anserina*, and in 6 with *Triglochin maritimum* and *Eleocharis uniglumis*.

In September, 1902, similar measurements were taken on the front beach at Freemantle, Western Australia. No vegetation occurred on the formation. The following results were obtained (Table II):

TABLE II

	2 cm.	5 cm.	10 cm.	20 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness 1–10
1....	32.6	25.4	22.9	20.2	26.4	13.4	9:00 A. M.	2	1
2....	37.4	28.7	27.1	24.9	30.1	14.6	1:00 P. M.	2	1.5
3....	26.2	19.2	17.4	15.6	27.5	12.9	2:00 P. M.	1.5	3
4....	25.4	20.4	18.5	15.8	24.4	12.5	11:30 A. M.	0.3	6
5....	21.3	15.6	14.2	13.6	22.7	12.8	12.15 P. M.	3.5	4

The average temperature of these five series at 2^{cm} depth is thus 28°.5 C., that is, 12°.1 higher than the mean of the previous series. The sea water in the latter case was much colder, while the atmospheric temperature was considerably higher.

Of sixty measurements taken in day time on the front beach under conditions as similar as possible, the highest temperature obtained for 2^{cm} depth was 42°.6 C. on the Queensland coast at Pialba, in Decem-

ber, 1901, while the lowest was 2°.1 near Mariehamn, Finland, in September, 1896. The average of these sixty observations was 18°.4 C.

The soil temperature on the middle beach is already much higher, as following data will show. The observations were made at the same time and in the same place as those mentioned in Table I. The distance from the water was 6.5^{m} and the sand pure quartz of medium size and yellow color.

TABLE III

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1.....	22.6	20.1	17.8	14.1	12.6
2.....	19.1	16.7	14.9	12.7	12.1
3.....	23.4	21.3	18.9	15.3	13.3
4.....	20.1	18.5	17.0	13.9	12.7
5.....	18.4	16.9	15.6	12.7	12.2
6.....	16.9	15.2	13.7	12.6	11.9
7.....	19.8	17.3	15.5	13.8	12.9

The vegetation consisted in 1 and 3 of an open community of the following constituents:

FACIES: *Leontodon autumnale*, copious.

SECONDARY: *Festuca rubra arenaria*, subcopious, *Agrostis vulgaris*, subcopious, *Plantago maritima*, gregarious, *Erythraea litoralis*, sparse.

In 2 Erythraea was scattered about in patches, between low shrubby *Alnus glutinosa*, solitary individuals of *Elymus arenarius*, and *Rosa canina*.

In 4, 5, and 7 a *Juncus Gerardi* community occurred on the middle beach, with sparse *Erythraea litoralis* and *Plantago maritima*. In 6 *Elymus arenarius* and *Festuca rubra arenaria* formed an open community.

A parallel table to Table II shows the temperature conditions on the middle beach at Fremantle, W. Australia. The sand was here fine, consisting of pure light-yellow quartz. Time and atmospheric conditions as in II.

TABLE IV

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1.....	35.2	23.4	22.4	20.7	18.4
2.....	38.6	25.8	24.6	23.6	20.0
3.....	29.5	18.6	18.3	16.5	15.8
4.....	27.2	21.3	19.6	17.2	16.3
5.....	24.6	16.9	16.1	14.9	14.4

A comparison with the results in Tables I, II, and III reveals the fact that, while the surface temperature (2^{cm}) in all cases was higher in the series given in Table IV than in Table II, the temperatures at 5^{cm} and lower were higher in the former case, presumably on account of a more intense evaporation, which caused a corresponding loss of heat. No such difference existed between Tables I and III, where the solar radiation was less, and both the atmospheric and sea-water temperature lower.

We shall now proceed to a statement of the temperature conditions on the upper beach. Table V gives the results of some observations made on that formation at Jerwe on the Oesel Island in the Baltic, in July, 1896. The beach has a low grade and is limited landward by a littoral dune in the shape of a steep and high bank, on the top of which small dunes are developed. The sand on the upper beach at the foot of this bank is rather coarse, consisting of a reddish-yellow quartz.

TABLE V

	2 cm.	5 cm.	10 cm.	20 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness
1 ...	22.4	22.8	21.4	19.6	21.6	17.1	10:30 A. M.	1	3
2 ...	27.3	26.2	24.5	22.7	25.2	16.4	1:00 P. M.	0.5	1
3 ...	26.8	24.3	22.8	21.1	23.6	16.1	3:15 P. M.	2	5

The next table is a continuation of the measurements given in Tables II and IV from Fremantle, W. Australia, and the general conditions supplied in regard to those tables refer also to these observations on the upper beach, except that the time in each case was about 15 minutes later. The sand was of medium-sized, white-yellow quartz, mixed with an abundance of shell fragments.

TABLE VI

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1.....	34.8	24.5	22.6	21.1	18.3
2.....	38.9	24.9	23.4	22.0	19.6
3.....	28.8	19.2	17.6	16.4	14.8
4.....	27.6	22.5	20.7	18.2	16.6
5.....	25.3	17.3	16.9	14.5	13.8

As will be seen, the temperature on this formation does not differ

essentially from that on the middle beach at the same locality as given in Table IV. The differences existing may be accounted for by the topography and by the fact that the upper beach here was covered with a sparse vegetation consisting of various low herbs.

On the littoral dune the temperature conditions are somewhat varying, usually higher on the landward slope, and a rise in temperature can also be noticed with an increase in the height of the dune. The summit and the landward slope of the littoral dune are frequently covered in large patches with vegetation, and the temperature differences between the open spots and those where plants occur are considerable.

Table VII shows a series of measurements made on the seaward slope of the littoral dune at Fremantle, W. A., under conditions similar to those given for previous observations from that locality. The sand was fine white quartz.

TABLE VII

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	35.2	26.4	23.5	21.5	19.2
2	38.8	27.3	22.6	20.6	18.4
3	29.4	20.5	18.1	16.2	15.4
4	28.9	21.3	19.4	17.7	16.2
5	25.6	18.7	16.6	15.1	14.3

Table VIII gives the temperature on the summit of the same dune, at a height of 6^m over the ocean level. The dune material consisted of medium sand, somewhat yellowish in color.

TABLE VIII

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	35.5	27.4	24.2	21.7	19.8
2	38.8	28.1	23.0	21.2	18.9
3	30.3	21.0	18.2	16.8	15.7
4	30.1	21.8	18.9	18.3	16.3
5	26.4	18.8	16.7	15.7	14.0

On the landward slope, some 3^m from the top, the following measurements were obtained:

TABLE IX

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1.....	35.4	27.0	23.6	21.5	19.4
2.....	39.2	27.6	22.8	20.4	18.2
3.....	29.8	20.8	18.1	16.5	15.6
4.....	29.5	21.7	19.0	17.8	16.1
5.....	25.9	18.9	16.8	15.6	14.3

In this last case the sand was rather fine quartz, of yellowish color. The maximum soil temperature measured by the author on a littoral dune formation was obtained in December, 1901, on the leeward slope of a high dune at Southport, Queensland, where the thermometer 2^{cm} under the surface registered 58°.4 C. at 2 P. M. The formation was devoid of vegetation.

The temperature of the dunes and the sand fields varies greatly. Some averages will be here given. Of the 34 readings made under general conditions as similar as possible a mean temperature of 26°.2 C. was obtained from dunes in Finland for a depth of 2^{cm} and 25°.4 for 5^{cm}. The average of 19 readings at Fremantle, W. A., was 28°.7 C. and of 12 readings at Southport, Queensland, 29°.8. On the dunes of North Cape, New Zealand, the author measured on the same day within one hour the following series: 26.1, 25.8, 24.2, 27.9, 25.4, 26.3, 26.1, 27°.9 C. The atmospheric temperature at the time was 25°.4, cloudiness 3, time December 7, 1902, 11:30 A. M.–12:30 P. M.

The daily variation of temperature must naturally be of some importance to the vegetation. Only a few observations have been made by the writer to this end. One series will be given as a sample of the extent to which such variations take place. The readings were made at Southport, Queensland, in December, 1901.

In the light of measurements obtained the local distribution of certain plants on the coastal sand formations seems to indicate that the temperature factor is of the greatest importance for the mode of association of plants into communities. On the coasts of the Baltic the writer made frequent observations which tend to show this.

At Åhus in Sweden there occurs on the upper beach an Ammophila-Elymus community, consisting of the following plants:

FACIES: *Ammophila arenaria, Elymus arenarius.*

SECONDARY: *Triticum junceum, Carex arenaria, Festuca rubra arenaria, F. ovina, Poa pratensis, Cakile maritima, Halianthus peploides.*

TABLE X

HOUR OF READING	ATMOSPHERIC TEMPERATURE	DEPTH UNDER SURFACE					CLOUDINESS 1–10
		2 cm.	5 cm.	10 cm.	20 cm.	50 cm.	
6 A. M.....	9°6 C.	4.9	4.2	5.7	9.1	14.3	6
7	10.8	6.5	5.6	5.9	9.4	14.4	2
8	11.4	7.7	6.9	6.2	9.4	14.6	3
9	15.6	9.0	8.9	6.9	9.6	14.6	1.5
10	17.7	11.2	10.2	8.0	9.7	14.5	4
11	19.5	14.6	11.8	9.6	9.8	14.5	3
12 NOON	23.2	17.2	13.0	10.5	10.1	14.7	3
1 P. M.....	26.3	19.6	14.3	11.8	10.7	14.4	5
2	27.2	19.4	14.8	12.6	11.4	14.5	4
3	27.0	18.1	14.6	12.7	11.6	14.5	4
4	26.4	18.0	14.3	12.6	11.8	14.4	5
5	25.1	17.3	14.0	11.8	11.6	14.5	4
6	22.3	15.1	13.5	11.2	11.7	14.6	2.5
7	18.6	12.9	12.3	10.4	11.9	14.6	1
8	16.2	11.0	10.7	9.5	11.6	14.7	0.5

The two species which constitute the facies of this community usually occur in small separated patches, and measurements of the temperature in the small sand elevations formed by these plants revealed the fact that in the Ammophila patches the soil temperature almost invariably was two-tenths to six-tenths of a degree higher that in the latter case, which would explain the lower temperature, but the exact difference in moisture has not been ascertained. Many similar instances of temperature differences have been noticed. *Halianthus peploides* always grows in colder places than *Argentina anserina*, although both together often form a community. This question of temperature differences influencing the formation of communities, however, needs further investigation before any decisive statements can be made. It must also be remembered that the temperature is influenced by the moisture, which in its turn depends to a great extent on the physical conditions of the soil.

MECHANICAL ANALYSIS OF SAND.—A considerable number of such analyses have been made by the writer, and a few series will here be given to show approximately the differences in size of sand grains on the various formations on different sand strands. In the table the

letter *A* refers to a series of samples from Kurische Nehrung on the northern coast of Germany, *D* to a series from sand formations near Amsterdam in Holland, *E* to sand from the west coast of France south of Bordeaux, *F* to samples from the west coast of Australia, near Fremantle, *G* to sand from Port Fairy, Victoria, *H* to the sand at Southport, Queensland, *I* to a series from North Cape of New Zealand, and *J* to a series of samples from the Pacific coast of North America near San Francisco.

	A	B	C	D	E
Submerged beach	Finest	Medium	Medium	Fine	Finest
Front beach	Fine	Medium	Fine	Fine	Coarse
Middle beach	Fine	Fine	Coarse	Medium	Coarse
Upper beach	Coarse	Medium	Coarse	Medium	Grits
Littoral dune	Medium	Fine	Medium	Fine	Medium
Dunes	Medium		Medium	Fine	Medium
Sand field		Finest			Finest

	F	G	H	I	J
Submerged beach	Coarse	Medium	Fine	Coarse	Medium
Front beach	Medium	Fine	Medium	Grits	Fine
Middle beach	Medium	Medium	Coarse	Coarse	Fine
Upper beach	Coarse	Medium	Coarse	Grits	Medium
Littoral dune	Medium	Fine	Medium	Medium	Fine
Dunes	Fine	Fine	Medium	Fine	Fine
Sand field		Finest			

In each of the above cases the result represents the average of 10 samples, secured at approximately corresponding places on each formation. As these data show, the coarsest sand occurs on the upper beach. The material that builds up the littoral as well as the ordinary dunes is usually of the same grade of coarseness. It is only when we analyze the sand from various places on the dunes that differences appear, which explain the formation of ripple marks and dunes as discussed on previous pages. It will be seen when we describe the vegetation on the various formations that the coarseness of the sand in some cases seems to determine the composition of the plant communities. This is easily understood when we consider that the size of the sand particles determines the water-holding capacity of the soil.

CHEMICAL COMPOSITION OF SAND.—The nutritive value of sand is different according to the chemical character of the sand grains. As

a rule, sand is very deficient in plant food, and this is especially the case with the commonest form of sand, that which consists mainly of quartz. The quartz grains are insoluble, or only to a very small degree soluble. Only in the case of lime or organic matter in the form of humus entering into the composition of the sand is there plant food in sufficient quantities to allow the development of a more luxuriant vegetation. Generally the chemical composition of coastal sands is very uniform, and this may to some extent account for the evident similarity in vegetation on these formations.

A number of analyses of sand have been made by the writer, and some typical results will be here related.

No. 1.—Middle beach, Eckerö Storby, Åland Islands, Baltic

	Per cent.		Per cent.
Insoluble matter	89.25	Alumina	1.38
Soluble silica	3.44	Water and organic matter	2.57
Lime	1.06	Nitrogen	0.16
Potash	0.18	Other constitutents	1.02
Phosphoric acid (soluble)	0.24	Total	100.01
Peroxid of iron	0.71		

No. 2.—Littoral dune, Engelholmshamn, Skåne, S. W. Sweden

	Per cent.		Per cent.
Insoluble matter	84.38	Alumina	1.83
Soluble silica	4.53	Water and organic matter	4.93
Lime	1.04	Nitrogen	0.12
Potash	0.21	Other constitutents	2.00
Phosphoric acid (soluble)	0.33	Total	99.99
Peroxid of iron	0.62		

No. 3.—Upper beach, North beach, near Perth, W. Austr.

	Per cent.		Per cent.
Insoluble matter	86.32	Alumina	0.93
Soluble silica	3.61	Water and organic matter	2.89
Lime	1.53	Nitrogen	0.03
Potash	0.36	Other constitutents	3.33
Phosphoric acid (soluble)	0.15	Total	100.02
Peroxid of iron	0.87		

No. 4.—Dunes, Southport, Queensland

	Per cent.		Per cent.
Insoluble matter	91.90	Alumina	1.08
Soluble silica	3.18	Water and organic matter	2.15
Lime	0.86	Nitrogen	0.11
Potash	0.21	Other constitutents	0.44
Phosphoric acid (soluble)	0.29	Total	100.00
Peroxid of iron	0.08		

No. 5.—Dunes, Golden Gate Park, San Francisco, Cal.

	Per cent.		Per cent.
Insoluble matter	88.27	Alumina	1.08
Soluble silica	4.42	Water and organic matter	2.15
Lime	1.94	Nitrogen	0.05
Potash	0.17	Other constitutents	1.80
Phosphoric acid (soluble)	0.08	Total	100.01
Peroxid of iron	0.05		

These analyses show what a small amount of plant food is available in the dunes in comparison with that in ordinary agricultural soil, where the insoluble substances do not comprise more than 70 per cent. of the total volume. And it must be remarked that the analyses here given represent soil from places more or less covered with vegetation, where the organic constituents are better preserved from decomposition and from being washed out by water than on open sand. They therefore show a higher percentage of humus and soluble material than the barren quartz unprotected from the influence of sun, air, and water. Where sand has recently been deposited after having been exposed for some time to sea water it is naturally very deficient in plant food, and it has therefore to be considerably changed before it is able to sustain a vegetation covering.

The amount of lime contained in the dunes varies to a great extent. On tropical coasts it is generally very large, especially where the sand is formed by disintegration of coral rocks. On such shores carbonate of lime is dissolved by the rain water and the sand is at a low depth under the surface consolidated into limestone. A similar process of calcification can be observed also on many coasts where the amount of lime is quite small, as on some coasts of Europe. Bang (1) has observed that the dune sand near the sea contains up to sixteen times more lime than farther inland. This is a natural result of the washing-out process and decomposition, which takes place on the open sand, and is more effective farther inland, because the supply diminishes with the distance from shore.

On the upper beach and on the seaward slope of the littoral dune are frequently found fragments of shells that have been carried ashore by the waves. In places where the littoral dune is broken, shells are often accumulated in the depressions, while more landward the lime in the animal remains is disintegrated by the carbon dioxid of the rain water.

The greater or smaller amount of peroxid of iron in dune sand determines to some extent its color. The usually colorless grains of pure quartz are covered with a thin coat of ferric hydroxid, which gives the sand its yellow color, and in some places almost a red tint.

THE SOLUBLE SALT CONTENT IN COASTAL SAND.—Of the soluble salts that saturate the coastal sands sodium chlorid is the most important. Its presence, as common salt, in all plants is well known, and its influence on the littoral flora is very apparent. Whether sodium chlorid is essential to plant life is still an open question, and the investigations hitherto conducted in order to ascertain this fact seem to indicate that such is not the case. In experiments it is difficult to eliminate salt entirely, but it has been conclusively shown that the smallest quantities only, if any at all, are needed for the development of plants, even for those which apparently prefer salty situations, when growing under natural conditions.

That common salt is injurious to plants, when present in excessive quantities, is certain. It is commonly believed that this unfavorable influence of salt is due to the amount of magnesium chlorid it contains. It is more likely, however, that all the chlorids are injurious, and experiments by the writer have supported this view, previously maintained by several authors.

It is generally stated by various writers that the formations on the sea coast contain a considerable amount of common salt. Thus WARMING (**14**) says that on the sandy beach the salty ground water is found at only a slight depth under the surface. CONTEJEAN (**3**), in speaking of the conditions in southwestern France, considers that his second belt of sea-shore vegetation, that is our middle and upper beach, is growing in a saline soil. MASCLEF (**9**) found the salt content in dunes near the sea to be 0.351 per cent., while at a distance 150^{m} from the shore he found 0.17 per cent. of sodium chlorid, and at 1500^{m} he discovered 0.041 per cent.

There has been some doubt, however, in the minds of certain authors whether the coastal dunes are impregnated with common salt or not. Among these is MASSART (**10**). The present writer has on various coasts made tests for salts in the sand by means of chemical analysis. The result of these observations shows that under ordinary circumstances *dunes do not contain sodium chlorids in perceptible*

quantities. When salt is found *it has been deposited as spray from the sea*, but this is rapidly washed out by rain water, and when no precipitation has fallen, the *sodium chlorid does not come into contact with the ground water but is detained on the surface by the upward movement of the water*. Because of this the roots of the plants are not exposed to sodium chlorid. On the littoral dune the uppermost half an inch layer of sand usually contains some salt, but deeper in the soil no salt is found before we reach the sea-level. The upper beach has very similar conditions, as a rule, except at times when inundated by high water. Even on the middle beach we cannot find that the sand would be impregnated with salt. On the contrary, for quite a considerable depth there is fresh water, which, on account of its being lighter than the salt water, flows on top of the latter. This fresh water is a part of the continuous stream of rain water, which slowly works its way to the sea. The roots of the plants do not, as a rule, penetrate deeper than to the bottom of this fresh-water layer, and it is therefore wrong to assume that the plants are growing in salt water on the beach. Even on the front beach, the layer in which the roots of the plants are situated has more of a brackish character, because the water from the beating waves runs off before it has time to sink through the layer of fresh water, which flows on the surface of the salty ground water.

On a superficial investigation of the beach it appears that the ground is thoroughly soaked with salt water, but careful sampling from various depths and subsequent analysis has made it apparent to the writer that this is not the case. It is a well-known fact, however, that the ash of strand and marine plants contains a much larger percentage of sodium chlorid than that of inland plants. This is due, of course, to the presence of a greater amount of salt on the sea shore than inland. But when it comes to a comparison between the conditions on sea shores and salt-impregnated formations in the interior, the amount of salt in the latter is much greater. This fact brings forward the question whether all sea-shore plants are halophiles or not. KEARNEY (**8**) has investigated this question and comes to the result that they are not. The present writer made numerous experiments in this direction and the results confirm those of KEARNEY, as the following discussion will show.

It has long ago been proved by experiments that most inland plants

are injured by the presence in the soil of sodium chlorid in certain quantities, which the strand plants are able to tolerate without evident injury. There appears to be a certain maximum amount of salt for every species, to which it is very accurately adapted, and this maximum cannot be overstepped without fatal results to the plant. In some cases investigated by the writer this maximum has been found to be:

	Per cent.		Per cent.
Argentina anserina	1.9	*Glaux maritima*	2.7
Aster Tripolium	2.6	*Juncus Gerardi*	2.2
Atripex hastata maritima	3.1	*Matricaria inodora maritima*	2.3
Cakile maritima	2.9	*Plantago maritima*	2.8
Crambe maritima	2.5	*Sonchus arvensis maritima*	2.6
Elymus arenarius	2.6	*Triglochin maritimum*	2.1
Erythraea vulgaris	1.9		

These experiments were conducted in the summer of 1894 with plants from the Baltic coasts. Sand cultures saturated with normal solution of sodium chlorid were used. In these cultures young seedlings as well as older plants were grown, and the results given above refer to seedlings, about two weeks old at the time of transplanting. They were grown in fresh water for five days, after which time the salt solutions were gradually applied. It was found that plants which had been growing on strands with low salinity were considerably more sensitive to an increase in the amount of salt than those which were brought in from the open shores with higher salt content in the water. Strong, well-developed plants adapted themselves more readily than weaker specimens to the gradual transfer to stronger salinity. It would be of considerable interest to ascertain whether this specific limit of salt concentration could be raised much higher by growing the plants through a succession of seasons. The ability of the seashore plants to endure salt in the soil without injury and by adapting themselves to these conditions has, no doubt, been the ultimate cause of their being in many cases confined to the strand, precluding competition from forms not possessing this power of resistance.

We also know from experimental cultures that strand plants do not need sodium chlorid in order to develop normally. The question then arises whether the common salt, even when present in quantities lower than the maximum, exercises a poisonous influence or not. SCHIMPER, who paid much attention to this matter, came to the con-

clusion that the chlorids produce abnormal conditions in the plants and disorders in the nutritive processes. In this regard most writers agree, but in explaining the means by which the plant neutralizes this injurious effect of common salt there is a wide divergence of opinion. While SCHIMPER maintains that the structural adaptations of halophile plants are caused by the necessity of keeping the relative amount of sodium chlorid in the cell-sap below the specific danger point, DIELS (**6**) considers that this is effected by chemical decomposition of the salt. This process is not known, but DIELS assumes that in respiration the succulent halophytes differ from other plants in that the oxidation does not proceed so far in halophytes, but stops at malic acid or some isomer, with which the cell-sap becomes saturated, while only small quantities of carbonic acid are evolved. The malic acid then combines with the hydrochloric acid and is excreted by the roots. BENECKE (**2**) has severely criticized these conclusions of DIELS.

In regions having a hot climate the evaporation of water is very great on the coastal sands and the salinity is naturally higher. The concentration of salts is also increased in countries where the rain falls only during a rainy period, leaving a long time in which no leaching of the salts takes place in the soil. In places with frequent rains the salts are rapidly washed out and carried deeper into the ground, until the lateral flow of water toward the sea is encountered.

The observations on salinity of strand sand made by the author are all based on chemical analysis. The electrical method of determining the salinity as employed by the United States Bureau of Soils was not familiar to the author at that time, but careful observations and determinations of the salinity with that method ought to reveal the causes of distribution of certain plants on the strand. The writer has found that *the small embryonic dunes formed by certain strand plants contain a greater amount of salts than those occupied by others.* Thus, for instance, the small, embryonic, *Elymus arenarius* dunes always contain 0.005–0.009 per cent. more sodium chlorid than the *Ammophila arenaria* dunes. Likewise the Mesembryanthemum dunes on the California coast have a higher salinity than the Abronia dunes, while the elevations formed by *Abronia latifolia* contain more salt than *A. umbellata* hummocks. These are the only examples which have been verified by analyses, but more extended investiga-

tions will, no doubt, give an explanation of certain hitherto unexplained features of the local distribution of strand plants.

We often find on sandy sea shores a number of immigrants from inland formations, and this occasional occurrence of plants which do not naturally belong to such habitat shows that it cannot be the chemical composition of the salt water that keeps so many island plants from the sea shore, but other adverse conditions, which allow only the peculiar sand-strand flora to develop. Even on the front beach, where the salinity is greatest, we cannot attribute the scarceness of the plants to the salt content, but to the easily movable sand soil.

As we have already mentioned, the lateral current of fresh water flowing on the surface of the salty ground water near the sea has to be taken into consideration when we discuss the salinity of the strand soil. Our assumption that the conditions of the strand are not such as to characterize this formation as halophytic is borne out by the analyses made of the salinity of the soil at different depths. Many true halophytes, of course, occur on the sea shore, but the strand flora as such must rather be classified as a halophile flora, while the true halophytes are those plants which are confined to saline situations in the interior, or where we know that the hydrodynamic conditions do not change to any marked degree the salinity, as is the case on the sea shore. If this holds good, the halophytes occurring on the strand must be regarded as immigrants from dry saline habitats.

Several Salsolaceous plants, widely spread in the interior of Australia, sometimes occur on the sea shores of that continent as straggling poor specimens, but reach their best development in the dry saline soil of the interior. SCHIMPER (**13**) maintains that the cliffs on the sea shore have a much less halophile flora than the sandy or marshy strands. This is evident to everyone who has studied the strand floras, but we shall find that the plants even on the cliffs exhibit many characters of the halophytes, and are sufficiently differentiated from the cliff vegetation of inland situations to warrant a classification as halophile. The physical nature of the substratum prevents its being impregnated with common salt. We have here to account for the development of adaptations so characteristic for halophytes, not so much through the influence of salt in the soil as through the salt

contained in the spray, to which the plants are constantly exposed. On sandy soils the protectional adaptations are caused more through the physical conditions of the sand, than through the salt content of the soil. The characteristic vegetation developed on all sand formations, inland as well as on the coast, is so much alike, that there is no reason to assume that the sodium chlorid content of the sea shore, which in fact is not very large, would be responsible for the aspect of the vegetation on marine sand strands. On coastal marshes the conditions are different, and this is also evident in the vegetation on such formations, which in no way differs from that on saline marshes in the interior, and always is composed of true halophytes.

A series of samples of the soil was taken with earth-auger on the beach and dunes at Fremantle, Western Australia, at various depths, and subsequently examined for soluble salts. The results appear in Table XI.

TABLE XI

Date	Formation	Distance from high-tide mark in meters	Character of soil	Depth in cm.	Angle of slope	Temperature ° C.	Degree of moisture 1–10	Percentage of salt	Notes
Dec. 18, '02	Lower beach, upper limit	2	Medium sand	20	15	18	9	0.005	
	Middle beach	5	Medium sand	35	21	20	6	0.004	Sparse vegetation
	Border of middle and upper beach	7	Coarse sand	30	23	20	6	0.004	
	Upper beach	10	Medium sand	30	26	22	4	0.009	
	Dune inside littoral dune	28	Fine sand	40	10	23	5	0.003	
	Littoral dune	15	Fine sand	40	30	21	4	0.007	
	Dune marsh inside littoral dune	29	Finest sand	20	0	19	10	0.005	
Dec. 21, '02	Middle beach	8	Medium sand	25	8	14	4	0.006	
	Same place	8	Medium sand	50	8	12	3	0.004	
	Upper beach	14	Medium sand	25 50	15	16 15	3 5	0.011 0.006	Sparse vegetation

DEVELOPMENT OF HUMUS.—There is no other soil which so little favors development of humus as the loose shifting sand. The organic substances that happen to be deposited on the sand are very rapidly decomposed by the admission of air, and the physical structure of the sand allows rain water to percolate and thus to carry the fine humus particles deep into the soil and out of reach of the roots. The earthworms, which are the most active agents in mold formation in forests, as DARWIN and MUELLER have shown, are entirely absent in sand and the mycorhizal fungi seem not to thrive on the beach, where they are likely to be exposed to occasional contact with sodium chlorid.

When a shrubby vegetation has got a foothold on the sand, the humus is developed to the best advantage. In the shade of the bushes remains of plants do not decompose so easily as on the open ground, they are more sheltered from the rain, and an accumulation of humus can take place, so that grasses and herbs are able to get a footing. When this has happened the sand is usually made permanently stable. The few animal remains that are thrown up on the front or middle beach enrich the soil on these formations only temporarily, and do not play any important rôle in the formation of the humus on the sand.

Topographic factors

The topography as a factor influencing the development of vegetation is very often overlooked by writers on plant geography. Its importance, however, is so considerable that it cannot be omitted in a discussion of the agents which exert their influence on plant life. On the vegetation topography acts principally indirectly, by determining to a great extent the moisture content of the soil, by influencing the temperature, the exposure to winds, and also the light relations. We intend here to mention briefly only the principal features of topography as far as they influence the conditions on coastal sand formations.

SURROUNDINGS.—From our previous discussion (**II**) of the development of the various sand formations it is apparent that the surroundings are of the greatest consequence to the evolution of dunes. On many of the coasts investigated the topographical conditions have been of such character as to prevent any greater development of dunes. Such was the case, for instance, on the southern shore of the

Gulf of Finland, where almost the whole shore line consists of a steep wall of rock, leaving only a narrow strip of beach along the water edge. In places where this rocky barrier was broken and the winds are allowed free play over a wider stretch of land, dunes appeared at once. The vegetation on the beach of the former type presents a somewhat different aspect from that on open shores with the background of a dune-complex. The best evidence of the influence of surroundings on the composition of the vegetation can be seen if we compare that on a sand field and on a dune-complex with its diversified topography. Also on the slopes of an unbroken dune, the vegetation is usually quite different from that on a train of dunes frequently cut through by furrows and valleys.

On beaches a similar difference can be noticed, and the cause underlying this effect can only be attributed to the topography. Where we have a long continuous beach the plants associate according to rules different from those which have determined the composition of the communities on cuspate forelands. This was especially evident on the shore stretches of sandy beaches that are so common on the shores of the islands in the Baltic.

ELEVATION.—This factor is of minor importance in regard to the sand-strand vegetation. The sand formations do not rise to any great height, but it seems that certain plants choose their place of growth with reference to altitude, even on these formations. Without taking into account the fact that humus naturally accumulates more rapidly in the depressions, we find that some plants prefer the foot of a dune, while others are found only on the middle of the front slope, and others again do not thrive except on the top of the dune, where they are constantly being covered with drifting sand.

On the beach a corresponding selection of habitat takes place. Some plants never occur on a low beach although the conditions otherwise seem to be favorable, but only a short distance away, where the beach rises more abruptly, they appear again. We have presumably two different causes for this. While on the dunes the selection of a place of growth is determined apparently by the plant's greater or less power of resistance against the drifting sand, on the beach the dominant cause must be the sensitiveness of the plant to inundations of salt water.

Depressions between the dunes offer to many plants a refuge from the sand-laden winds, and the richer soil in the troughs induces other plants to settle.

GRADE OF SLOPE.—We have elsewhere (**11**) referred to this factor as being of great moment in the growth of dunes and in the development of sand formations generally. Its influence on the moisture conditions is of no less importance. The higher up on the slope the drier is the soil, the greater the evaporation, and the more intense the influence of the wind.

The exposure of the slope is another matter of the greatest consequence to the vegetation on the sand formations. The various degrees of slope ought always to be considered when a description of a habitat is given in order to arrive at a correct understanding of the conditions that have determined the composition of the plant community. Southern slopes in the northern hemisphere and northerly slopes in the southern are drier than those facing other directions, and the vegetation has a corresponding aspect. On sea coasts the exposure to the prevailing winds has to be noticed.

Light relations are further to a certain degree determined by the direction of the slope, and this is of special importance in northern latitudes, where light even during the period of growth is not too abundant.

Historical factors

Under this heading we include all those factors whose influence on plant life is determined by time. This must not be understood as if time was not involved in the action of other factors, but that the period of influence and the time required for attaining any results is of such a long duration, that it cannot be ascertained within a few generations of plants. Physiographical changes of land and sea, whether within a century or within long geological periods, have to be considered in this connection. One of the most important historical factors to be looked upon in explaining the present conditions on sand strands is the oscillation of the coast line. The erosion of the shore by waves and the deposition of sand or other material are equally important. Sand deposits are in many places formed so rapidly that the effect can be noticed within a very short time. The influence of animals, principally through grazing, and the interven-

tion of man belong strictly to the group of biotic factors, but have here been considered in connection with the historical factors as a matter of convenience.

OSCILLATION OF THE COAST LINE.—Many coasts are slowly rising, while in other instances the coasts are sinking. We have excellent examples of both kinds of movements on the Baltic. While the whole coast of Sweden north of Stockholm, and the coasts of Finland are in a state of elevation, the southern shore of the Baltic is in a corresponding state of depression. Besides having a great influence on the development of dunes, this oscillation of the coast line has had a marked bearing on the evolution of the flora on the coastal sands.

On the shores mentioned which are rising, one may see in some instances how long stretches of land are slowly raised above water and in a few years carry a cover of vegetation that gives an instructive demonstration of the successive stages of development of the plant associations. Again, on the sinking shores of the southern Baltic may be frequently found examples of plant communities being destroyed in the course of a few years through the submersion of the shore.

On the coasts bordering upon the oceans oscillations also take place, but they are usually neither so regular nor so rapid as these changes on the Baltic.

In postglacial times considerable changes of the coast line of the Scandinavian countries have taken place, and as we are able to follow these changes with the assistance of fossil remains of plants, found in old sea beaches now raised high above the present level of the sea, we can to some extent interpret the various stages of development which have been passed before the flora arrived at its present state. This question will be discussed in another paper.

EOLIAN DEPOSITS.—The influence of the wind on formation of plant communities on the coastal sands is shown not only in the peculiar arrangement of the plants in patches, but also in the aspect of the aggregations of plants, which (especially in the case of trees and shrubs) give evidence of being continuously attacked by the strong winds laden with spray or sand. Shrub associations on open strands are usually lower toward the shore, gradually increasing in height inland under the shelter of the more exposed specimens.

Most of the sand-strand plants are not able to withstand partial burying by the shifting sand; consequently it very often happens that

FIG. 1.—*Cupressus macrocarpa* on Cypress Point, Monterey, Cal., showing influence of wind. (Photograph by author.)

FIG. 2.—Rejuvenated Salix dune at San Francisco, Cal. (Photograph by author.)

whole communities are suddenly destroyed and their place taken up by plants able to endure more or less complete covering by sand. Sometimes it may be observed that trees, which are being buried by

an encroaching dune, are bent leeward (*fig. 1*). The cause of this is to be found in the continuous pressure, or in sudden gusts of wind which bend the trees while the onrushing sand prevents return to the original position. As a rule the sand on the lee side of a dune is moister, and the slope is consequently steeper. Often slides of sand take place, and they also bend or even break the trunks of the trees.

Dunes which have been made stable by a cover of plants are sometimes again broken up by the wind (*fig. 2*). Such formations are often met with on the Baltic coasts. On these broken-up dunes the usual series of development of vegetation begins anew and thus

FIG. 3.—Embryonic dunes inland from littoral dune, south of Cliff House, San Francisco, Cal. (Photograph by author.)

they have a peculiar character, remnants of the old communities being mixed with the new immigrants. A new life-history of the plant community is started, and during the course of development it may take a direction entirely different from the former series.

Vegetation covering on the ground will greatly slacken the speed of the air current which comes into immediate contact with the ground, and if bushes or other obstructions are in the path of the wind, dunes are often formed behind them (*fig. 3*). The plants that are first struck by the whole force of the wind are mostly injured, not only by its mechanical action, but to a greater extent

by the sand carried by the wind. While the wind in itself dries the plant, the sand particles, which often have a high temperature, are still more apt to increase the evaporation, and thus to hinder the development of the plant (*fig. 4*). Further, stems of plants growing on exposed places on coastal sands are often eroded by the sand, and even the green leaves are sometimes cut into shreds during severe storms by the sharp angular sand grains.

FIG. 4.—Effect of wind on *Leptospermum scoparium* Forst. on dunes at New Brighton, Canterbury, New Zealand. (Photograph by Dr. L. COCKAYNE.)

OTHER SEDIMENTS.—As we have pointed out in another place sand is especially likely to accumulate in the neighborhood of river mouths, and in such places heavy floods often carry down and deposit on the sand considerable quantities of mud, which then enrich the soil, and cause the appearance of a quite new flora, that soon will exclude the true sand plants.

On almost all marine coasts quantities of seaweeds are thrown ashore by the waves, but in warm climates they are so rapidly decomposed and the remains washed away, that no accumulations can be

effected. In more temperate regions, however, these seaweeds lie in banks on the beach for some time, and add to the fertility of the

FIG. 5.—Bank of Macrocystis on the beach at New Brighton, Canterbury, east coast of South Island of New Zealand. Height of scale 41 cm. (Photograph by Dr. L. COCKAYNE.)

FIG. 6.—Kelp banks on West Australian coast. (Photograph by author.)

soil. *Figs. 5* and *6* show such kelp banks from the coasts of New Zealand and West Australia.

Along the shores of the Baltic a considerable amount of seaweeds,

principally *Fucus vesiculosus*, is deposited on the beach at high-water mark. On open shores these banks mark the limit of vegetation toward the sea, and are characterized by a vegetation quite different from that on the rest of the beach.

MAN'S INTERVENTION.—The principal influence of man on coastal sand floras is a result of his endeavors to arrest the drifting of sand. This is mainly done by planting so-called sand-binding plants, or by covering the loose sand with refuse or other material. Either action brings about a considerable change in the natural development of the sand vegetation.

Near cities the sand dunes are sometimes used for supplying sand for industrial purposes, and in such cases the removal of the sand will naturally change the conditions for the original vegetation. Fires are sometimes started through the carelessness of man, but as the natural vegetation is very seldom dense, the influence of fires on sand formations on the coast is not great, except in artificial plantations.

Grazing animals do more injury to the sand vegetation by tramp ling and uprooting the plants than by actual feeding on them, and in the neighborhood of many cities, where sandy beaches and dunes occur, human agency is equally detrimental to the plant covering.

Summary

Summing up the physical conditions prevailing on the various sand formations on marine coasts we would say that *the submerged beach* is always covered with water, and therefore is the most salty of all the formations. The soil is loose, the temperature that of the sea water, and the surf is continuously beating. The vegetation is therefore especially adapted to these conditions, and in most cases no plants at all are able to gain a footing on this formation.

The front beach is periodically washed by the waves, presenting alternating terrestrial and aquatic conditions. It is almost constantly exposed to the spray and has a salty ground not very deep under the surface. The soil is very loose, still more so than on the submerged beach. Strong insolation, rapid evaporation, and a constantly changing temperature are characteristic. It is on account of these adverse conditions usually devoid of vegetation, with the exception of a few unicellular algae, often Cyanophyceae, but where

the formation has not been inundated for a few days only the spores of the algae retain their vitality. On the Baltic coasts where the salinity of the sea water is low, conditions approach more or less those on fresh-water shores, and many green algae occur in the sand. The width of the barren front strand varies not only with the slope, but also with the force of the surf.

When a higher vegetation occurs on this formation it is open and

FIG. 7.—Middle and upper beach south of Cliff House, San Francisco, Cal. On upper beach small dunes made by *Cakile americana*. In background littoral dune with Ammophila. (Photograph by author.)

very poor. The loose soil, the wind, and the impact of the surf place a limit on the types that are able to develop. These are mainly annuals or perennials with long creeping rhizomes and the flora is always poor both in species and individuals.

The middle beach is characterized by its light color, its abundant moisture, its low salinity, its loose soil, and its comparatively low temperature. Occasional inundations, spray, and wind are the direct causes of the scattered vegetation, consisting mainly of annuals

or a few perennials. These plants also are more or less dwarfed, because of the wind and the cold substratum. The tension line between this and the following formation is very marked. Some-

FIG. 8.—Ammophila dunes at San Francisco, Cal. Embryonic Salix dune to the left. In winter. (Photograph by author.)

FIG. 9.—Grassy littoral dune, north of Fremantle, Western Australia. (Photograph by author.)

times a transition belt can be distinguished, marked by a darker strip of humus-mixed sand, and covered with a denser vegetation (*fig. 7*).

The upper beach has a higher percentage of humus, abundant moisture, and a higher temperature than the middle beach. The illumination is much greater, especially during certain times of the day, when the formation is not shaded by the littoral dune. Evaporation and radiation from the soil, however, are less intense, because the

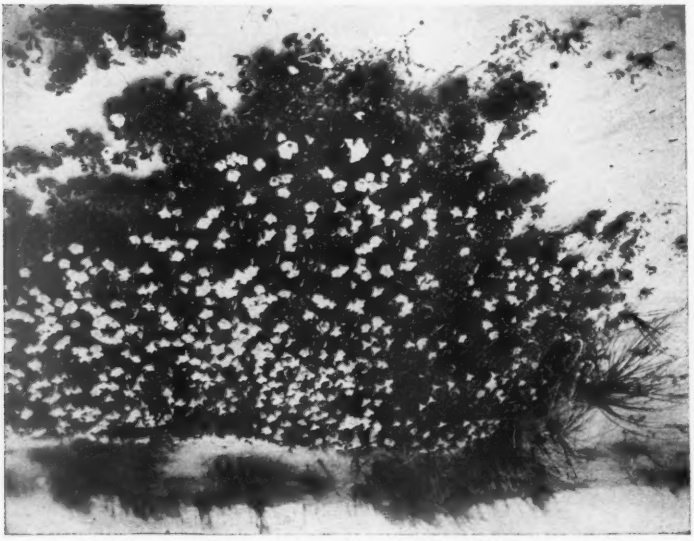

FIG. 10.—Soldanella community on dune slope at New Brighton, Canterbury, New Zealand. On summit, *Scirpus frondosus*. (Photograph by Dr. L. COCKAYNE.)

ground is well covered with plants. The amount of spray is less the farther we go from shore, and complete inundations occur only at very long intervals. The distance to the salty ground water is considerably greater than on the lower formations, and very few true halophytes appear on this belt. The influence of wind is very marked in that sand is blown from the middle beach over this formation, which often is covered with small embryonic dunes (*fig. 8*). The wind favors transportation of seeds and shoots from the middle

FIG. 11.—Sand dunes at Studeli Mile in north Jutland, Denmark, covered by *Elymus arenarius*, *Ammophila arenaria*, *Carex arenaria*, etc. In the foreground especially *Salix repens*. (Photograph by Dr. F. BÖRGESEN.)

beach, and in many cases the occurrence on the upper beach of plants belonging to the middle beach can only be explained by their having been blown landward from the original position.

The vegetation on the upper beach consists principally of perennial herbs, shrubs, or low trees. The tension line toward the littoral dune is not so marked as in the direction of the middle beach, but where no dune formations are developed the upper beach usually borders upon a forest. In the latter case it often happens that inland plants have wandered out to the sea-shore formations, while it never happens that sea-shore plants have been able to establish themselves inland on the meadow or forest that usually follows the strand formations.

The littoral dune is much exposed to the wind, its moisture content is low, constant oxidation of organic water goes on, and the temperature is lower than on the upper beach, because of more intense radiation. The soil is very loose, shifting, and sterile (*fig. 9*). The vegetation shows the results of these conditions very plainly. It is prostrate and dwarfed in habit, scattered and poor in variety of forms.

The active dune (the white dune of WARMING) has all the characteristics of the littoral dune in excess, and its vegetation is generally still more monotonous. Some difference can be observed in regard to the plants on the slope and summit of the dunes. It is usually richer in species on the latter part of the formation.

The stationary dune (the gray dune of WARMING) is formed at a greater distance from the sea, where the sand has to some extent consolidated, and a heather vegetation has been established. Formation of humus goes on, the plants grow closer and closer, mosses or lichens occupy the ground between the higher plants, and finally the soil is completely covered with a carpet of vegetation. This heather association is the final stage in the series of sand-plant communities beginning on the small embryonic dunes to leeward from the littoral dune (*fig. 11*).

The sandy field is richer in humus than any of the former sand formations mentioned. It has a comparatively level surface, is better able to retain moisture, and has a higher temperature. The sand grains are of such uniform size as to prevent ripple or dune formation, and

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FIG. 12.—Sand field at Lodskovvad Mile in north Jutland, Denmark. The place was formerly a shallow lake, which had been filled in with sand three years previous to the time (August 18, 1898) when the picture was taken. The vegetation consists of *Salix repens*, *Juncus balticus*, *Agrostis alba maritima*, *Eleocharis palustris*, and *Phragmites communis*. In the background sand dunes with Elymus and Ammophila. (Photograph by Dr. F. BÖRGESEN.)

the vegetation covering is consequently developed in quite a different way from that on dunes (*fig. 12*).

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SOME ASPECTS OF AMITOSIS IN SYNCHYTRIUM[1]

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(WITH PLATES III AND IV)

Previous papers on the cytology of Synchytrium have announced very striking peculiarities in the nuclear behavior of this interesting fungus. The idiosyncrasies, only a portion of which have yet been described, are so abundant at a certain period of the life-cycle of the plant that it is very difficult to consider any one set of phenomena without quickly becoming involved in all the rest, either because of the occurrence of different types of structures in the same coenocytic cyst, or because of transitional forms apparently connecting diverse structures. While no final interpretation of any one series of nuclear transformations can be made until it has been brought into relation with the whole life-history, it is apparent that it is out of the question to work out all of the peculiarities at once. The present paper is an attempt to isolate and describe one of the most conspicuous groups of nuclear phenomena. Further correlation of this with other manifestations of nuclear activity will be undertaken in later papers.

As in the preparation of a former paper on Synchytrium (GRIGGS **7**), the writer is under very great obligations to his friend, Professor F. L. STEVENS, for the information which aroused his interest in the problem and for criticism of the results. This obligation is increased by the fact that Dr. STEVENS also supplied the material from which the slides were made. The present paper deals entirely with one species, *Synchytrium decipiens* Farlow. The drawings have all been taken from preparations stained with Heidenhain's iron alum hematoxylin. The triple stain has also been used.

In the cytology of this plant there is no more striking feature than the variation in the size of the nuclei. In the same cyst nuclei are frequently found ranging all the way from 8 or 10 μ down to 1 μ in diameter, as was first reported by STEVENS (**12**, *fig. 2*). Very often the small nuclei are bunched together, either in a close morula-like

[1] Contributions from the Botanical Laboratory of the Ohio State University, No. XL.

cluster (*fig. 33*) or in a looser group (*fig. 18*). The origin and fate of these small nuclei is the subject of the present paper. Although such variations in the size of the nuclei are sometimes found in almost any stage of the period of nuclear division, they are most conspicuous immediately after the division of the primary nucleus and continue prominent until there are 200–300 nuclei in the cyst. It is at this same stage that the other peculiarities in the cytology are most pronounced. While this period of irregularities is not sharply marked off from the succeeding phases of the life-history, yet as the nuclei become more and more numerous there seems to be a tendency for them to settle down, so to speak, and to conform more nearly to the usual habits of dividing nuclei in growing tissue.

The isolation of these groups suggests that their constituent nuclei have a common origin. Because of the absence of any pairing, and because of their great differences in size, one is inclined to suspect that they have been derived by some process other than mitosis. Since mitosis in this plant is always simultaneous, involving all the nuclei in a cyst, the differences could not be due to the failure of some nuclei to divide, while their neighbors became smaller and smaller by repeated division. They might of course be due to some process of mitosis in which the products were unequal, as in the reduction division of an animal egg. But all the mitoses observed gave rise to equal daughter nuclei. Further, mitoses in cysts of this age are uncommon. This led STEVENS (**12**) to suggest the possibility of an amitotic origin for the nuclei of this stage.

There are several processes of direct nuclear division in Synchytrium. Two of these are quite different from the commonly observed division by an amoeboid constriction of the parent nucleus. While they may be considered under the general term amitosis, which has come to include several forms of non-mitotic division, they require distinctive terms for their designation. Indeed, there is considerable need for a classification of the different forms of direct division, especially in view of the increased importance amitosis is likely to assume in future cytological discussion. The first process, which consists of a budding-out of a small nucleus from a larger, may be designated *nuclear gemmation*. The second differs from ordinary amitosis in that the nucleus loses its membrane and vacuole of karyo-

lymph before the division, which is a multiple fragmentation. This form of division I shall term *heteroschizis* (ἕτερος, different, and σχίζειν, to split).

NUCLEAR GEMMATION

In nuclear gemmation, as is usual in amitosis, the division of the chromatin is not nearly so frequently observed as the separation of the two nuclei. In the resting nuclei of Synchytrium the whole of the chromatin content is usually concentrated in a single globular karyosome (nucleolus). At the beginning of nuclear gemmation the margin of this karyosome becomes crenate, and rounded lobes develop, which separate from it and become smaller independent karyosomes (*figs. 4–8*). Sometimes only one daughter karyosome migrates from the parent at a time (*fig. 6*); sometimes the parent undergoes a process of bipartition resulting in equal daughter karyosomes (*fig. 7*); or sometimes several form at once, in which case the whole karyosome breaks up (*fig. 4*). *Fig. 8* shows a very large nucleus where the daughter karyosomes were unusually numerous. They were not free in the nucleus, as appears from the drawing, but all of them were lying against the nuclear membrane, only one hemisphere of which is represented.

After the separation of the small karyosomes is complete, *they migrate through the nuclear membrane*. This process is probably rather gradual, since all stages are easy to observe: *figs. 8, 19* show them lying loosely against the membrane; in *figs. 9, 20* they are pressed against it; in *figs. 8, 21* they have begun to pass through; *fig. 21* shows one lying almost exactly half-way through the membrane; *figs. 10, 11* show karyosomes which have passed through, but still lie close against, the membrane.

As soon as the passage is completed, a vacuole, similar to the cavity of the parent nucleus, appears around the migrating karyosome. This is quickly surrounded by a membrane, extending out from the wall of the parent nucleus into the cytoplasm next the vacuole (*fig. 10*). This process can be observed satisfactorily only when the daughter nucleus is of considerable size, because of the delicacy of the membranes of the smaller nuclei. When the membrane is complete the new nucleus moves away from the parent and becomes an independent

small nucleus free in the cytoplasm. The stages in this process are also easy to follow: *figs. 3, 9, 11* show cases where the karyosome is still in contact with the membrane of the parent; *figs. 6, 12, 13, 18* cases where the karyosome has separated from the parent, but the membranes remain in contact; *figs. 3, 5, 9, 14* cases where the two nuclei have separated, but still lie close together.

Division by nuclear gemmation occurs also in the spirem stage (*figs. 15–17*). In this case the division of the chromatin takes place at the time of spirem formation and cannot be definitely connected with nuclear division, but the manner of the separation of the daughter nuclei is the same as that already described. *Figs. 1, 2* show groups of small nuclei from a cyst where all the large nuclei (*fig. 16*) are in spirem.

In cysts where the nuclei are numerous and evenly scattered through the cytoplasm it can be seen that the peripheral nuclei divide much earlier than the central ones. Groups of small nuclei are always found at the periphery before the large nuclei in the center are much divided. Thus a lateral section of a cyst (*fig. 1*) shows only uniform groups of small nuclei, while the central sections show numerous large nuclei, of which *fig. 16* is an example.

Nuclear gemmation may take place at very different rates in different cysts. In the cyst from which *figs. 11, 12, 14* were taken, the few small nuclei present are scattered singly through the cytoplasm. In this case the appearances indicate a slow and orderly formation of small nuclei. In other cysts the chromatin seems to be extruded with almost explosive violence (*figs. 24–26*, cf. also GLASER **6**). In these cases a large proportion of the migrating chromatin never forms nuclei but degenerates in the cytoplasm. Some members of almost every large group are imperfect and disintegrate, forming in their last stages deeply staining spots in the cytoplasm. Such disintegration is seldom seen in cysts where the small nuclei give evidence of more gradual formation. It is more pronounced in younger cysts where there are only a few parent nuclei, than in later stages where they are numerous.

The deeply staining granules on the nuclear membrane vary from karyosomes half the size of the mother karyosome to microsomes similar to those usually found in the nuclear membrane in both

animal and plant cells (*figs. 7, 18, 21, 22*). No optical distinction can be drawn between these extremes. The very smallest granules, however, do not form small nuclei but may function in metabolism. In mitosis and in the degeneration of the large nuclei (*fig. 22*) they are cast aside with the old nuclear membrane and lost in the cytoplasm. But no distinction can be drawn between these granules and those which form small nuclei, for some of the latter are excessively minute. Besides these, there are yet other granules on the nuclear membrane from which conspicuous radiations proceed into the cytoplasm as from centrosomes (*fig. 39*). The discussion of these bodies involves other questions than those considered in the present paper and cannot be undertaken here. Another complicating factor is the frequent presence of asters near nuclei which are giving off gemmae. I have avoided using such cases for the figures of the present paper, but in many instances nuclei adjoining those drawn had conspicuous asters, and it would be possible to duplicate most of the drawings herewith given from nuclei showing asters. But though the centrosome problem, one aspect of which was touched in a former paper (GRIGGS **7**), is very puzzling and far from solution, my belief is that it is independent of the phenomena discussed in the present paper.

HETEROSCHIZIS

The second process of amitosis is a multiple division or fragmentation of the nucleus, which occurs for the most part at later stages than nuclear gemmation, but is sometimes found in young cysts (*fig. 33*) and rarely also even in segmented cysts (*fig. 34*). Nuclei derived by heteroschizis are at once distinguished from those due to nuclear gemmation, because they form not a loose group but a close morula-like cluster, as figured by STEVENS (**12**, *fig. 3f*). As in nuclear gemmation, all the stages in their formation are easy to observe and may be found in a single cyst. But while the new nuclei are formed one at a time in that process, here they originate simultaneously by the fragmentation of the mother nucleus. The first indication of division consists in the loss of the nuclear membrane and the vacuole of nuclear sap, leaving the karyosome lying naked in the cytoplasm, like the chromosomes in the metaphase of mitosis (*fig. 27*). The karyosome then apparently enlarges to nearly double its former size (*fig.*

28). This statement is based on the fact that the naked karyosomes are, in the cases observed, larger than those of any other nuclei in the same cysts, and that the resultant clusters of small nuclei are greater in mass than any single nucleus in the cyst at this stage. The variation in the size of the nuclei, however, is so great in other stages that it is not impossible that these may have been larger nuclei in the beginning. Lobes (*fig. 29*) now appear on the margin of the karyosome, each of which rounds off and becomes the karyosome of a small nucleus. When these karyosomes have separated, vacuoles of nuclear sap appear around them; surrounding membranes are next formed in the meshes of the cytoreticulum bounding the cavities, thus completing the process. The membranes, however, do not appear simultaneously around all the nuclei of a cluster. There is usually sufficient difference to allow some observation of the process of membrane formation. The vacuoles which become the nuclear cavities are at first indistinguishable from those between the meshes of the cytoreticulum which are filled with cell sap, but they are gradually surrounded by membranes which are apparently precipitated from the cytoplasm next the cavity. Neither in heteroschizis nor in nuclear gemmation is there evidence of any connection of the centrosomes with membrane formation such as occurs in the reconstruction of the nucleus after mitosis (KUSANO **8**, GRIGGS **7**).

Besides the two sorts of amitosis just described, a third method has been observed a few times. In this process, which has been seen only when the nuclei were in spirem, the nucleus becomes strongly lobed; each lobe contains a portion of the original unchanged spirem; the lobes become more pronounced and are cut apart by continued constriction. There may be only two lobes, as in ordinary amitosis, or there may be several, as in heteroschizis. Although even a single nucleus of this kind (*fig. 40*) would seem to indicate the general nature of the process, there is much concerning it which is doubtful, and its occurrence is rare in my slides. I refrain, therefore, from more than mention of the matter at this time.

LATER HISTORY OF THE SMALL NUCLEI

If amitosis leads to degeneration and death, as has been held almost universally until recently, we should expect to find a large

percentage of degenerating small nuclei in every cyst where they occur, either during the period of their formation or later. After nuclear gemmation, however, degeneration of chromatin is relatively small in amount and is almost altogether confined to masses which never organize nuclei. It occurs not in the later portion of the period of gemmation but only during the early portion, when there are few large nuclei in the cysts. In clusters due to heteroschizis, degeneration may also occur at later stages, but is infrequent at any time. If, on the other hand, these amitoses are due to pathological conditions affecting the whole parasite, we should expect to find a large number of dying cysts. Fully three-fourths of all the few-nucleate cysts give evidence of amitosis. Of the remainder only a small number show mitoses at this stage. This hypothesis would therefore require that three-fourths of the cysts should degenerate sooner or later. But no such thing occurs. Degenerating cysts are seldom found, and the degeneration gives no indication of being connected with earlier amitoses.

The clusters of small nuclei arising from heteroschizis tend to remain close together, and when mitosis is resumed they may form a cluster of small spindles. *Fig. 35* shows such a cluster between prophase and metaphase, in which the remains of the nuclear membranes are still evident. Below them is the solitary spindle of a large nucleus, of which there are 40–50 in the cyst. *Fig. 36* shows three objects from another cyst assembled in one drawing. At *a* is a similar cluster of small spindles; at *b* is one of the solitary spindles of the larger nuclei, all of which in this cyst are in a later phase than the clusters; at *c* is a deeply staining mass which has the appearance of a cluster similar to *a* degenerating. *Figs. 37, 38* show similar clusters in anaphase. Although the spindle fibers in *fig. 38* are distorted so as to give somewhat the appearance of a pathological multipolar spindle, some of the spindles are perfectly normal. The spindles of *fig. 37* resemble closely the solitary spindles of the cyst and are typical examples of the peculiar anaphases of this genus.

The groups of small nuclei arising by nuclear gemmation scatter quickly, so that there is no means of connecting them with the mitoses which occur later. They have the usual relations, however, to the cytoplasm and appear normal in all microscopic characters. When

not too small they bud off other small nuclei in the same manner (*fig. 18*). This process usually continues till all the nuclei in the cyst are approximately equal in size (*figs. 1, 2*). Sometimes all the daughter nuclei given off are so much smaller than the parent that the mother karyosome is never divided up among the daughters, but remains behind full size, after giving up its chromatin, like the nucleolus in the prophases of mitosis. In this case the *large nuclei* degenerate and leave the small ones as the functional nuclei of the cyst. *Fig. 20* shows the first indication of this in the vacuolate karyosome of the parent nucleus. In *fig. 21* all the chromatin has migrated from the old karyosome but some of the small karyosomes still remain inside the nuclear membrane. The larger of these are about the same size as the numerous small nuclei of the cyst. *Fig. 22* shows another large nucleus from the same cyst, which is entirely bereft of chromatin. *Fig. 23* is the last stage of the process; here the old nuclear membrane has disappeared and the faintly staining old karyosome (nucleolus) lies naked in the cytoplasm. Beside it is shown one of the functional nuclei. We are therefore led to the conclusion that the nuclei derived by these processes of amitosis are normal, and that they with their descendants become the functional nuclei of later stages, capable of perpetuating the species.

GENERAL CONSIDERATIONS

Although the processes by which these nuclei are derived are novel, the formation of normal tissue by amitosis is by no means without parallel. C. M. CHILD (**1–5**) has recently shown that amitosis is a frequent occurrence in regenerating organs, embryos, and in some adult animals. He records instances from most of the great animal phyla, including coelenterates, flat worms, trematodes, cestodes, insects, amphioxus, fishes, amphibia, and birds. In these cases, contrary to what would be expected, there seems to be no especial distinction between the soma and the germ plasm as to the origin of the nuclei. In Moniezia, a tapeworm infesting sheep, which CHILD has worked out most fully, the germ plasm is almost exclusively derived by amitosis and the spermatogonia may even undergo a sort of amitotic reduction by which sperms are formed without ever having passed through mitosis. In general, amitosis is most common in

regions of excessively rapid growth, where the nuclei are small and have scant cytoplasm, while the larger nuclei, better supplied with cytoplasm, divide by mitosis. This leads CHILD to conclude (**5**, p. 292): "In short I am inclined to believe that amitosis is associated with conditions where the demand for material or perhaps for some particular substances exceeds the supply." The behavior of the nuclei of Synchytrium is distinctly opposed to the generalization of this hypothesis, for in Synchytrium amitosis is most marked when the nuclei are largest and the ratio of nuclei to cytoplasm is at a minimum. While a condition of "hunger" may very well be assumed to exist in the cells of a rapidly regenerating organ or in a growing embryo, it cannot be ascribed to a dividing cyst of Synchytrium, because growth is very slight after the division of the primary nucleus, while the supply of nutriment from the host is presumably as great as before.

But in all of these cases the conditions of growth demand an excessively rapid multiplication of nuclei, and indicate that the process of nuclear reproduction is pressed on so rapidly as to give no opportunity for the rhythmic pause occasioned by mitosis. If the stimuli to growth and reproduction are independent, as many observations indicate, we may suppose that when the stimulus to division becomes excessive the nucleus divides directly, without waiting for the long preliminary pause necessary in mitosis. If the stimulus were but slightly stronger than in mitosis, a slow and orderly division of the chromatin would result, and the daughter nuclei would be mostly perfect; but if the stimulus became greater the process would be accelerated, until finally the nucleus would explode and a large proportion of the chromatin would never succeed in forming new nuclei at all. This is exactly in line with CHILD'S view that amitosis is an orthodromic process which ". . . . pushed to the extreme must always result in the total destruction of the original substances," so that "it is not strange that degeneration frequently follows amitosis, but there is no reason for supposing that it must always follow, and the facts prove that it does not." While this hypothesis may not cover cases of pathological amitosis, which superficially would seem to accord with the hunger hypothesis, it would afford a basis for associating the non-mitotic divisions in Synchytrium with those in regenerating members, embryos, and other rapidly growing tissues.

Knowledge that in certain instances the reproductive cells of a species are independent of mitosis for their origin must affect current theories of heredity, which, since the renaissance of MENDEL'S law, have leaned very heavily on the individuality of the chromosomes and their separation in the reduction division. CHILD rejects the chromosome theory in any universal application. He believes (p. 290) that "these processes appear to consist essentially in the production of new nuclear material like that already present and without the periodical recurrence of metamorphosis. The act of division is very probably a mere incident of the increasing volume of substance." Accordingly he is inclined to doubt the constancy of the chromosome number in the tapeworm, although he feels that the facts are too difficult of determination to admit of certainty. In Synchytrium, likewise, the minuteness of the nuclei makes determination of the chromosome number so difficult that one hesitates to dogmatize. But in all the many cases in which the chromosomes could be counted on the spindle the number seemed to be constantly four (cf. *fig. 36b*). The same number was given provisionally by STEVENS (**13**) in his first paper and is shown by the drawings of his second paper (**12**). This matter may, however, be left for consideration later, after the mitoses have been worked out in detail. But whether the chromosome number is found to be constant or variable, it is obvious that our theories of heredity will require considerable revision.

SUMMARY OF RESULTS

The numerous peculiarities in the cytology of Synchytrium occur mostly in a somewhat definite *period of irregularities* immediately following the division of the primary nucleus.

In this stage direct division of the nucleus is more frequent than mitosis. This takes place by at least two processes:

1. *Nuclear gemmation.*—The karyosome of the parent nucleus gives off a small karyosome which migrates through the nuclear membrane, forms a vacuole and a membrane about itself, and becomes an independent small nucleus, the whole looking like a budding yeast plant. This process is repeated until the parent nucleus is converted into small nuclei, often forming a definite group.

2. *Heteroschizis.*—The membrane of the parent nucleus dissolves,

and the karyosome fragments into a number of pieces, each of which becomes a new nucleus, thus giving rise to a morula-like cluster of nuclei.

These nuclei at later stages undergo mitosis and their descendants form spores and become the nuclei of succeeding generations.

No variation in the number of chromosomes in any of the nuclei of the plant has been detected.

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EXPLANATION OF PLATES III AND IV

The figures were all made with a Spencer 1.5^{mm} immersion objective and compensating ocular 12, giving a magnification of 2130, excepting *fig. 1*, for

which ocular 2 (magnification 355) was used. They were reduced ⅓ in reproduction, canceling the enlargement due to the camera and rendering them the same size as they were seen in the microscope.

PLATE III

FIG. 1.—A lateral section of a cyst, showing numerous groups of small nuclei due to nuclear gemmation.

FIG. 2.—One of the groups shown in *fig. 1*.

FIGS. 3–6.—The breaking-up of the mother karyosome preparatory to the migration of the chromatin.

FIG. 7.—Bipartition of the mother karyosome to form equal daughters.

FIG. 8.—Nucleus with a large number of daughter karyosomes lying on the nuclear membrane, only one hemisphere of which is shown.

FIG. 9.—A nucleus with one of the daughter karyosomes pressed against the nuclear membrane; three small nuclei which have budded off from it near by.

FIG. 10.—Daughter karyosome constructing its nuclear cavity and membrane.

FIG. 11.—Daughter nucleus complete but still closely appressed to the membrane of its parent.

FIGS. 12, 13.—Karyosomes of daughter nuclei separated from the parents but their membranes still in contact.

FIG. 14.—Daughter nucleus separated from its parent but lying close by.

FIGS. 15–17.—Nuclear gemmation from the spirem stage. (*Fig. 16* is one of the large nuclei from the center of the cyst from which *figs. 1* and *2* were taken.)

FIGS. 18–20.—Resultant groups of small nuclei.

PLATE IV

FIGS. 21–23.—Stages in the degeneration of the parent nuclei.

FIGS. 24–26.—Nuclei from which chromatin has been thrown out in large quantities and is mostly degenerating without forming new nuclei.

FIG. 27.—Beginning of heteroschizis; nuclear membrane dissolving, karyosome slightly irregular.

FIG. 28.—Membrane and nuclear cavity lost, karyosome much enlarged. Same cyst as *fig. 27*.

FIG. 29.—Karyosome lobed. Same cyst as *figs. 27* and *28*.

FIGS. 30–32.—Karyosomes broken up, nuclear membranes appearing around the daughter karyosomes. (*Fig. 32* is from the same cyst as *figs. 27–29*.)

FIG. 33.—A very large cluster complete.

FIG. 34.—A single segment from a summer sorus whose nucleus has divided by heteroschizis.

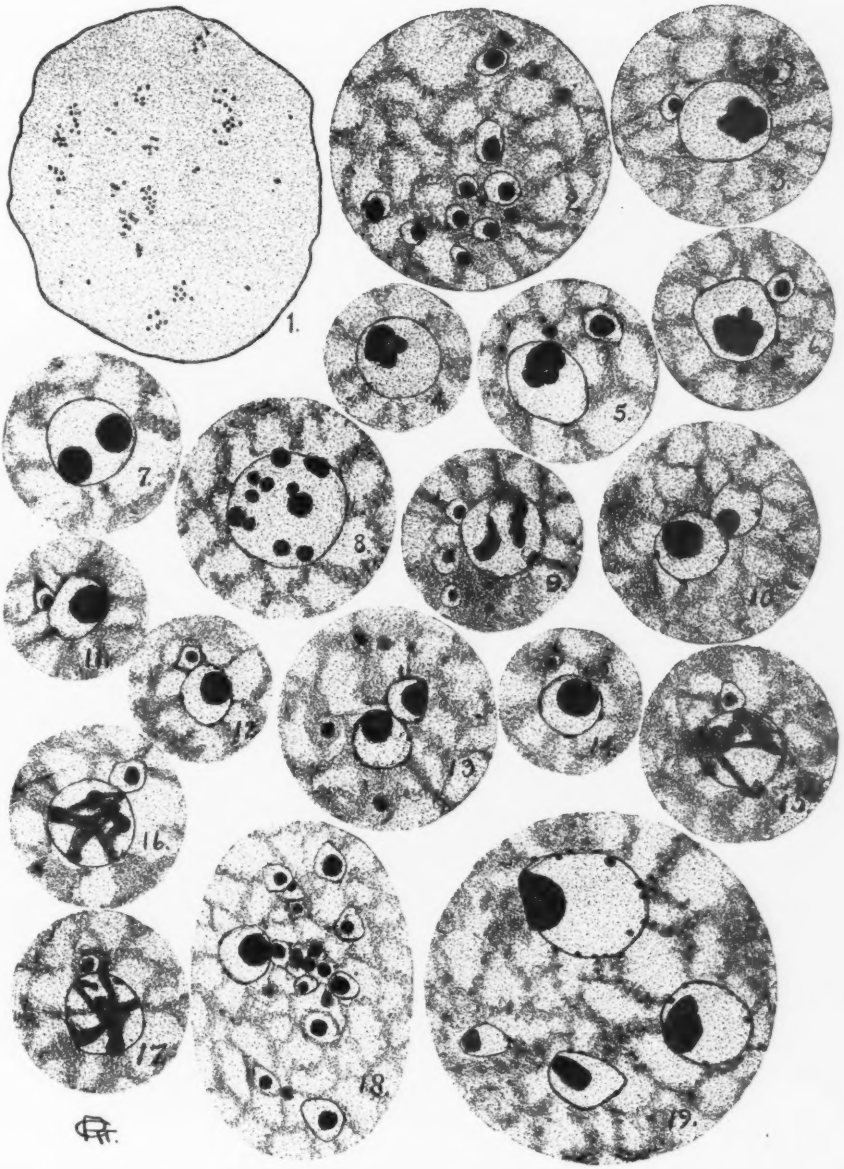
FIG. 35.—A cluster of spindles arising from the division of such a cluster as *fig. 33*, together with a single spindle of one of the solitary nuclei of the cyst.

FIG. 36.—*a*, a cluster of spindles similar to *fig. 35*; *b*, a solitary spindle from the same cyst; *c*, probably a cluster of spindles disintegrating.

FIGS. 37, 38.—Similar clusters of spindles in anaphase.

FIG. 39.—A nucleus with deeply staining granules on its membrane, from which radiations are given off into the cytoplasm.

FIG. 40.—A nucleus fragmenting by constriction.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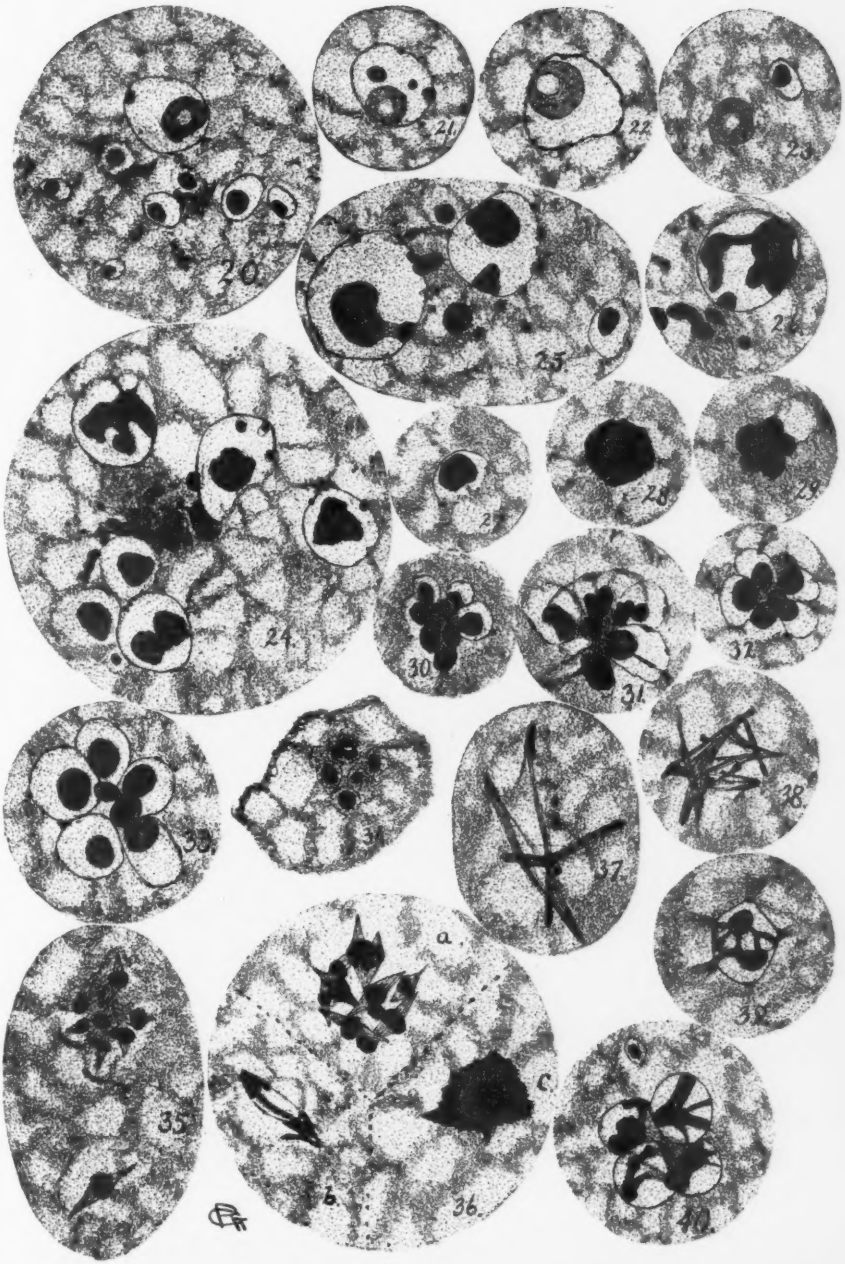
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VASCULAR ANATOMY OF THE SEEDLING OF *MICROCYCAS CALOCOMA*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 122

HELEN ANGELA DORETY

(WITH PLATES V AND VI)

HISTORICAL

DECANDOLLE (5) in the first account of the genus Microcycas expresses the opinion that it holds a position among cycads intermediate between Dioon and Zamia.

A historical sketch of the literature concerning *Microcycas calocoma* may be found prefacing the taxonomic account of the species by CALDWELL and BAKER (1), who succeeded in procuring material from Cuba. The only part of their description which concerns us here is the statement that the stem has a single vascular cylinder.

In a second paper, intended primarily to present the conditions in the reproductive structures, CALDWELL (2) has described incidentally some of the superficial characters of the embryo and seedling. Certain details, which he naturally overlooked in so comprehensive a work, have been brought to light by a more detailed study having the seedling alone as its object.

INVESTIGATION

In the first place, it is not the root which is seen to emerge from the seed and bend downward, as described and pictured by this author; the sequence of events in the process of germination is the same as that described for Ceratozamia (7), the same which occurs in the other cycads which I have germinated, *Dioon edule*, *D. spinulosum*, and species of Zamia. The root is not yet formed when the base of the elongating embryo ruptures the seed coat in the small, less indurated, micropylar region. When it emerges, it still bears the small brown disk constituting the only remains of the coleorhiza, an organ which, in the early stages of the embryogeny, is by far the larger portion of the sporophyte. The united cotyledonary stalks bend downward toward the soil. The root may not pierce the coleorhizal disk until the latter

has touched the soil; indeed its appearance in some seeds is preceded by the exit of the plumule.

A second detail in which this description must differ from the one cited is that the usual number of cotyledons is only two. They never wholly emerge from the seed. Their common stalk, which forms a sheath about the plumule, is soon ruptured in many places by the radial growth of the latter, and its decay causes the seed to drop away.

The appearance of embryos of Microcycas, like those of Ceratozamia described by CHAMBERLAIN (**3**), examined at short intervals during the period between fertilization and germination, indicates that there is no resting stage; and if at any time the seeds are allowed to dry, the embryos are killed. LAND (**10**) relates that he has reason to suspect the same condition in Ephedra.

CALDWELL has called attention to the adhesion of embryo to endosperm. This adhesion is greater than in any of the cycads I have studied, except Zamia. So intimate is the union, that by using ordinary precautions, one does not separate them entirely, but always carries some few layers of the endosperm through the microtome and stains with sections of the embryo.

Coincident with the close adhesion of embryo to endosperm is the remarkable fusion of the cotyledons. Although these always arise as two distinct organs, the fusion in older embryos is so complete that several were sectioned from the apex to within a distance of 0.5^{mm} above the tip of the plumule without discovering any trace of the characteristic seam made by the meeting of the adaxial epidermal layers (*fig. 1*). The epidermal cells themselves disappear in many cases slightly above the meeting of the inner faces over the plumule. The seam was not seen to extend to the surface at any level in these embryos, although there were conspicuous superficial sutures (*fig. 1*) in some of them. The plumule is liberated by the splitting of the sheath into strips, each of which simulates the petiole of an individual cotyledon. To my knowledge so complete a fusion of cotyledons has not been reported of a cycad.

Each cotyledon may have eight or ten vascular strands; all are collateral, with normal orientation. Apparent exceptions may occur immediately above a dichotomy or immediately below a fusion or an

approximation. In these situations, the xylem of one strand faces that of the other, giving to the inner one an inverse orientation (*d*, *figs. 1, 2*). When the fusion of two bundles is complete, the combination presents the appearance of a single concentric strand.

All the cotyledonary traces are derived from the branching of three, which join the central cylinder (*fig. 3*) in a manner similar to that described by MATTE (**11**) and THIESSEN (**12**) for *Dioon edule*, and by the present writer (**7**) for Ceratozamia. The wood remains endarch as far out as the sheathing base of the cotyledons (*fig. 13*); it becomes mesarch in this region; and in the upper portion of the blade the wood in the greater number of the strands is exarch. Transfusion tissue is abundant, and in close connection with the centripetal xylem. Mucilage ducts alternate with the cotyledonary traces. Tannin cells are conspicuous in the peripheral region.

The hypocotyl has no vascular plate, no protostele; the passage from stem to root is therefore easily studied. The four cotyledonary strands remain distinct throughout this portion of the axis, only fusing laterally with the few elements of the leaf traces still remaining to form a very imperfect siphonostele. Their elements finally unite with those of the four root poles. The metaxylem and phloem divide, as usual, and the resulting portions swing to right and left, the right half of the phloem of each joining with the left half of that of the next, with sometimes the lowermost extremities of leaf-trace phloem intervening (*fig. 4a*). There is thus produced the characteristic root structure, four groups of phloem alternating with four double-fan-shaped xylem groups. Irregular proliferation of the medulla often separates the phloem group again into its two constituents (*fig. 6*).

In the cortex of the hypocotyl were discovered the remains of a very broken zone of cambium. No traces, however, of any vascular tissue could be detected outside the central system in seedlings with two expanded leaves and several others developing.

The root in all the seedlings under observation was tetrarch (*figs. 4a, 6*) with a reduction to triarch toward the tip, in some cases. Mucilage ducts are numerous in the hypocotyl, but do not penetrate into the root. Neither pericycle nor endodermis is distinct in these

young roots. The root tip differs in no observable respect from that of Ceratozamia.

In the stem four large groups of leaf traces alternate with the cotyledonary strands, just above the cotyledonary node (*fig. 3*). Higher up (*fig. 7*), they close in, and together constitute the central cylinder of the axis. Taking a generally vertical course, these traces branch and anastomose until they reach a position so near to the growing points of leaf and stem that the vascular tissue is still procambial. In this position, even before the procambial strands from leaf and stem apex have united, the traces destined for the leaf margins manifest the phenomenon of girdling.

At first the wood of the leaf traces is endarch. *Fig. 8* represents a portion of a leaf-trace girdle, and *fig. 9* a cross-section of two vertical strands from the middle of the same leaf at the same level. *Figs. 10, 11* illustrate stages in the transition from the endarch to the mesarch condition. The wood becomes exarch at a relatively low level in some of the foliar strands, and there is considerable irregularity in different traces in this respect. *Fig. 12* is a drawing of one of the traces (*b*) in *fig. 14*, still in the region of the stipules. The other traces of the same leaf retain, at this level, a few elements of centrifugal xylem; this strand is entirely destitute of them. Further—and I have attempted to represent it diagrammatically—the wood in all the traces of this petiole is more nearly exarch than in those of the older leaf (l^2), although the section of that leaf which is here represented is higher up in the petiole than that of the younger leaf. In spite of such irregularities, however, the statement holds that the xylem is entirely centrifugal near the base of both cotyledons and leaves, and that it gradually diminishes to the vanishing point in proportion to the appearance and increase of centripetal xylem in the ascent of the cotyledonary blade and leaf petiole.

The section represented by *fig. 13* is very close to the leaf bases. It shows the increase in the number of bundles entering consecutive leaves, and also the meriphyte's gradual assumption of the Ω arrangement from the open arch of the early leaves. Transfusion tissue is present in these traces.

The strands are all collateral. Frequent branchings and approximations occur, and real fusions are common, most noticeably of those

strands which are brought to the center of the meriphyte and form the flanks of the Ω. When two of these strands are fusing, the centripetal elements of both xylem groups are gradually eliminated and the protoxylem groups are therefore brought together and finally united. This common group of protoxylem, then, is surrounded by the united metaxylem, and outside of this the phloem of both bundles may almost encircle the xylem, completing the delusion of a concentric bundle (*figs. 15, 16*).

Mucilage ducts occur in stem and leaves. They sometimes extend through the petiole as far as the bases of the pinnae.

The characteristic cycad ramentum is prominent, especially upon the unfolded leaves. The hairs are one-celled. *Fig. 18* shows the tip of a young pinna bearing these epidermal outgrowths.

Tannin cells occur in the periphery of the petiole, and may extend well into the pinnae. They are in close relation with the mechanical tissue, as represented in *fig. 17*.

DISCUSSION

The suppression of one of the cotyledons of Ceratozamia illustrates one process by which the monocotyledonous condition may be reached; the fusion of these organs in Microcycas affords an illustration of another method, one in harmony with the well-known theory of Miss SARGANT. Experimentation with some of the monocotyledonous dicotyledons listed by COULTER and CHAMBERLAIN (**5**) shows that in at least some of them the former process has taken place.

But this fusion of the cotyledons of Microcycas has a further meaning to one engaged in the study of a series of juvenile gymnosperms. The free lobing at the tips of the cotyledons in so many cycads seems to me to represent an ancestral condition of polycotyledony. Many embryos of Zamia and *Dioon spinulosum* in my collection have four to ten of these lobes, extending, in some cases, three-fourths of the length of the cotyledon. A young embryo of *Dioon spinulosum* with four cotyledons, and one of *Pinus edulis* with twelve cotyledons in four well-marked groups have a remarkable similarity. Of course, the pine cotyledons soon escape from the small, comparatively dry endosperm and thin seed coats, and develop exteriorly to their full

size, which is *in toto* much greater than that attained by the two cotyledons of a cycad. But let the conditions be such as to cause in the pine seed the production of the massive endosperm and indurated coats that characterize the cycad seed; and let the cotyledons be confined within the moist endosperm until they attain their full size, with the pressure of this growth forcing them into such intimate connection with it as to cause difficulty in distinguishing between them, and bringing the tips of the cotyledonary vascular strands into intimate contact with the endosperm, a condition reported by WORSDELL for *Cycas revoluta* (**13**) and by THIESSEN for *Dioon edule* (**12**): under such pressure, the inner faces of the pine cotyledons would be very intimately united and the question naturally suggests itself, What would become of the epidermis of these inner faces?

The alternation of mucilage canals with the cotyledonary vascular strands in cycads, and its ready relation to the peculiar condition found in pine cotyledons, may be used as evidence for a theory of fusion as well as for one of splitting, as HILL proposes (**8**).

The absence of the protostele in the hypocotyl of Microcycas in contrast to the condition found in *Dioon edule* and Ceratozamia may not have any significance in the light of recent investigation. That the protostele is, in general, the most primitive condition of the vascular axis may be true; but that this structure must occur in every primitive vascular plant is, of course, not true; neither are we to regard as primitive all plants in which it is found. CHRYSLER (**4**) has found it in members of the Araceae. There are other characters, however, which seem to indicate a greater advance than that made by Cycas or Encephalartos, or even Ceratozamia. These are the single stele and the degree of elimination of the cortical cambium, which, in the cycad stems, produces this vascular tissue. However, the large proportion of centripetal wood in the foliar traces is an offsetting primitive character, which must be weighed in the same balance.

The undoubted polyspermy would seem, at first sight, to bear down the weight of evidence on this side; but it is possible that this primitive feature is a recurrence rather than a direct inheritance: what JEFFREY calls a coenogenetic, rather than a palingenetic, character. JUEL (**9**) found as many as twenty sperms in the pollen tube of *Cupressus Goveniana*, and no one can believe that Cupressus has

retained this primitive feature when all the closely related genera have discarded it.

However that may be, this curious combination of characters, and the absolutely unique archegonial development, are features to be reckoned with by those who, in the future, when all the evidence is in, will be in a position to decide upon the phylogenetic place of Microcycas.

What is to be thought of the early appearance of girdling is scarcely worth saying until we learn something definite concerning the cause of girdling itself. The theories now in the field approach only remotely to the causes lying at the foundation of the phenomenon. It is probable that it may be relegated, like so many other problems, to the domain of cytology. That cell division takes place much more frequently in the horizontal than in the vertical direction in every portion of the axis is clearly evident.

SUMMARY

1. There is no resting stage in the development of the embryo of *Microcycas calocoma*.

2. The germination is hypogean.

3. The root is a delayed organ, as in Dioon and Ceratozamia.

4. There are two cotyledons as in all cycads (except, perhaps, Encephalartos).

5. The cotyledons are often fused to form one organic whole, the plumule escaping by bursting the sheath.

6. Mucilage ducts alternate with the 8–10 cotyledonary strands.

7. The cotyledonary node is similar to that of *Dioon edule* and Ceratozamia, but the vascular cylinder of the hypocotyl is a siphonostele.

8. The hypocotyl contains no cortical vascular tissue, although there are remnants of a broken-up cambial zone.

9. The vascular strands of cotyledons and leaves are endarch at base and exarch in the upper portions. The exarch condition obtains throughout most of the length of the petiole.

10. Girdling of the marginal leaf traces takes place while the tissue is procambial.

11. The root is tetrarch, but may reduce to triarch toward the tip.

Grateful acknowledgments are due to Professor JOHN M. COULTER, and Dr. W. J. G. LAND, under whom the investigation was conducted, and to Professors CHARLES J. CHAMBERLAIN and OTIS W. CALDWELL for material.

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EXPLANATION OF PLATES V AND VI

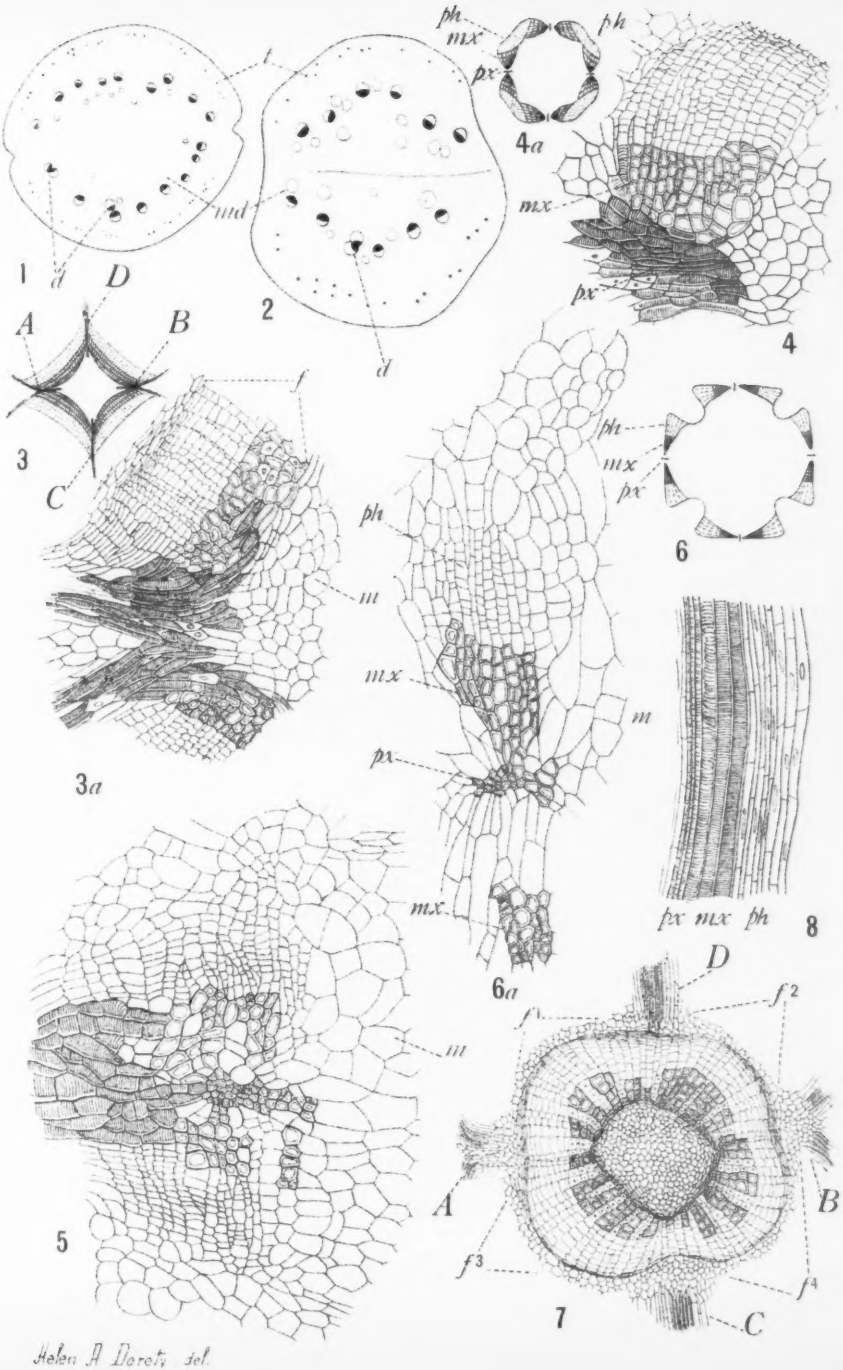
The drawings were made with the aid of an Abbé camera lucida. The following abbreviations have been employed: *A*, *B*, *C*, *D*, main cotyledonary traces; *cs*, cotyledonary sheath; *cfx*, centrifugal xylem; *cpx*, centripetal xylem; *cx*, cortex; *e*, epidermis; *f*, group of leaf traces; *l*, leaf; *m*, medulla; *md*, mucilage duct; *mx*, metaxylem; *ph*, phloem; *px*, protoxylem; *r*, ramentum; *t*, tannin cells.

PLATE V

FIG. 1.—Transverse section near the middle of the cotyledons, showing their complete fusion and the large number of cotyledonary strands. ×8.

FIG. 2.—Transverse section of cotyledons 0.6^{mm} above the tip of plumule. ×8.

FIG. 3.—Diagram of stele 40 μ above the cotyledonary node.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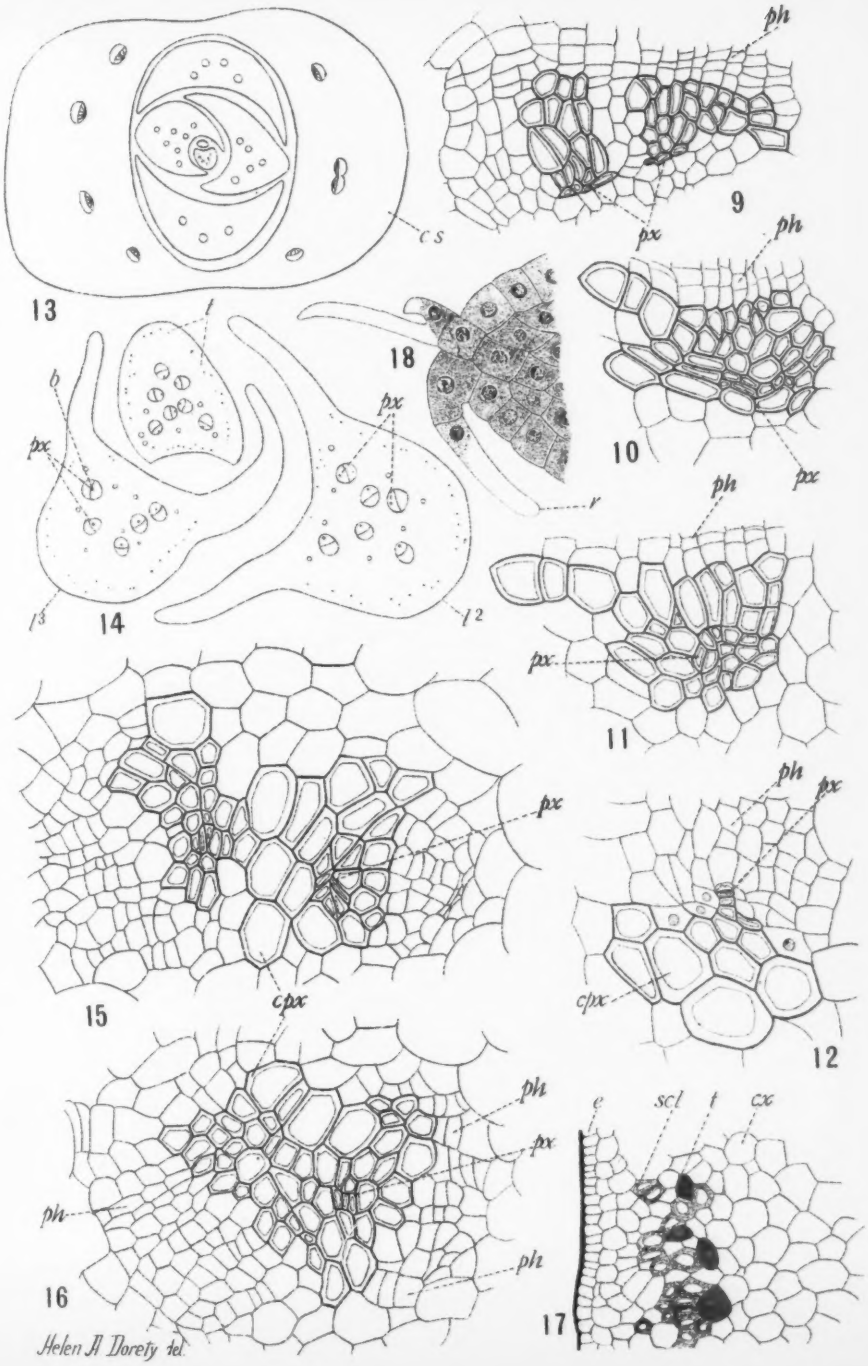
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FIG. 3*a*.—Detail from *fig. 3* showing one of the four cotyledonary traces near its point of insertion. ×60.

FIG. 4.—Base of the cotyledonary trace shown in *fig. 3a*. ×60.

FIG. 4*a*.—Diagram of stele of hypocotyl showing method of formation of root arrangement.

FIG. 5.—Exit of lateral root. ×60.

FIG. 6.—Diagram of root stele.

FIG. 6*a*.—Detail of one of the root poles. ×60.

FIG. 7.—Transverse section of the central vascular system above the cotyledonary node. It is composed of four groups of leaf traces. Semidiagrammatic.

FIG. 8.—Longitudinal section of portion of girdling leaf trace taken from transverse section of seedling. ×60.

PLATE VI

FIG. 9.—Transverse section of median traces of same leaf from same section as *fig. 8*. ×380.

FIG. 10.—Transverse section of leaf trace slightly above that represented in *fig. 9*. ×380.

FIG. 11.—Transverse section of same bundle 60 μ above section represented in *fig. 10*. ×380.

FIG. 12.—Exarch bundle from petiole 8^{mm} from base. ×380.

FIG. 13.—Transverse section of embryo, showing the sheath formed by the fusion of the cotyledonary petioles, the increase in the number of leaf traces in consecutive leaves, and their gradual assumption of the Ω arrangement. ×8.

FIG. 14.—Transverse section of three leaves in their natural arrangement, showing the relative amount of centrifugal wood at different levels of the petiole. ×8.

FIG. 15.—Approach of two leaf traces. ×380.

FIG. 16.—Fusion of some of the xylem elements of same to form a quasi-concentric strand. ×380.

FIG. 17.—Portion of peripheral region of tissue of petiole showing position of tannin cells. ×380.

FIG. 18.—Tip of young pinna showing unicellular hairs or ramentum. ×760.

BRIEFER ARTICLES

THE NATURE OF BALANCED SOLUTIONS

In his recent "Note on balanced solutions"[1] Professor LOEW criticizes some of my statements. The following reply is inspired solely by the desire to obviate if possible any misunderstanding regarding the nature of a balanced solution.

A balanced solution is defined by LOEB as one in which the toxic effects which each salt would have, were it alone present in solution, are inhibited by one or more antagonistic salts in the solution.

Professor LOEW objects to the term toxic as applied to calcium and potassium salts. His statement that I and a pupil claim to have discovered the poisonous action of potassium and calcium respectively is evidently due to a misapprehension. On the contrary, we treated them as fully accepted facts, and it was a surprise to us that he should call them in question. The poisonous action of a salt must be determined by comparing its effects with those of *pure* distilled water, or, in the case of strong solutions, with the effects of an isotonic balanced solution or an isotonic solution of an indifferent substance, if such can be found. In the absence of the facts needful for such a comparison, it is not possible to say whether the effects observed by him are to be regarded as toxic or not. At the concentration chiefly used in my experiments (.12 *M*) roots of wheat reached a length in KCl of 63^{mm}, in $CaCl_2$ of 84^{mm}, in an isotonic balanced solution of 360^{mm}, and in distilled water of 740^{mm}. I may add that for certain forms of Vaucheria KCl and $CaCl_2$ at the dilution of .001 *M* (or even less) may be toxic, inasmuch as they kill the algae in three or four days, while in distilled water or dilute sea water of a hundred times greater osmotic pressure, they remain alive for many weeks. For such forms the components of Knop's solution including the K and Ca, taken individually, would prove poisonous. But for such plants as wheat the concentration of Ca and K used in Knop's solution is too weak to be regarded as toxic.

Professor LOEW's designation of Knop's as a balanced solution seems, to say the least, very misleading. In a balanced solution the components are poisonous when taken separately. But Professor LOEW tells us that neither calcium nor potassium salts are to be regarded as poisonous. They are important constituents of Knop's solution. How then does he regard it as a balanced solution? Only it would seem (since here the

[1] BOT. GAZETTE 46:302. 1908.

toxicity of the anions is negligible) by supposing that the sole poisonous constituent is magnesium, whose toxic action is completely inhibited by the calcium present. But on this view it is clear that the potassium and iron are completely superfluous from the standpoint of a balanced solution. Knop added them for nutrient, not for balancing, purposes, nor is there reason to suppose that he was aware of antagonistic salt effects. At the concentrations at which he worked these effects are not at all evident with such flowering plants as were used in his experiments. Under these circumstances the discovery of antagonistic salt effects is very improbable. For most of the plants for which Knop's solution is employed at its ordinary concentration, it is not a balanced solution, because its individual components are not sufficiently toxic to require balancing.

That to Professor LOEW is due the very great credit of investigating the antagonistic action of magnesium and calcium, and of making clear its economic importance, is acknowledged by all. These and other investigations made by him in the difficult and obscure field of the function of the mineral salts are of the highest value. Together with the experiments of other investigators they have thrown much light on antagonistic action. Inasmuch, however, as Professor LOEW apparently does not believe in generalizing the principle of antagonistic action, as Professor LOEB has done in his theory of balanced solutions, but prefers to restrict it to the single case of Mg *vs.* Ca, I find myself quite unable to agree with him. In the course of a series of experiments on wheat I have found antagonism between each of the following pairs of salts:

NH_4 *vs.* Ca	NH_4 *vs.* Na	Mg *vs.* K	Na *vs.* Sr
K *vs.* Ca	NH_4 *vs.* K	Na *vs.* Ba	K *vs.* Sr
Na *vs.* Ca	Na *vs.* K	K *vs.* Ba	Mg *vs.* Sr
Mg *vs.* Ca			

One who has to deal with such a series of facts can hardly be expected to adopt a view which accounts for only one of these cases and ignores the rest, or explains them as due to the formation of double salts, particularly as such an explanation is wholly untenable in view of the facts of dissociation.—W. J. V. OSTERHOUT, *University of California, Berkeley.*

THE EXTRAFASCICULAR CAMBIUM OF CERATOZAMIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 123

(WITH PLATE VII)

The anatomical features presented by the seedling of Ceratozamia described in a previous paper (3) gave promise of such phylogenetic importance that the study has been continued upon older stems. The interest centers mainly in the extrafascicular cambium—its origin, its distribution, and its failure to differentiate xylem and phloem which could be clearly recognized as such. In a careful examination of microtome sections of over eighty seedlings, varying in age from a few months to two years, only one small extrafascicular bundle was found.

The origin of the concentric vascular zones of cycad stems puzzled the early anatomists. BRONGNIART (1), failing to distinguish the phloem in these zones, regarded them as the equivalent of the seasonal wood rings of dicotyledons. VON MOHL (8) said that they were an aggregation of bundles which passed out from the central cylinder and, running downward in the cortex, grouped themselves in a ring. LESTIBONDOIS (4) saw individual bundles in the cortex, but thought they foreshadowed the breaking-up of the central stele, and so considered the cycads as a transition group from dicotyledons to monocotyledons. METTENIUS, to whom we are indebted for much of our knowledge of cycad anatomy, made no attempt to explain the extra vascular zones. CONSTANTIN and MOROT (2) thought that the tissue arose from the pericycle.

All the early research was confined to mature stems of Cycas and Encephalartos. In 1890, SOLMS-LAUBACH (7) reported the absence of such zones in *Ceratozamia mexicana*. In 1896 WORSDELL (9) added Macrozamia to the list of cycads in which these thickenings occur, and in 1898 (10) recorded their absence from the stem of Stangeria; in 1900 (11) he found them in the root of *Bowenia spectabilis*. His study of seedlings of species of Cycas (10) demonstrated to WORSDELL that the extrafascicular zones in mature stems arose as independent cortical cylinders arranged in distinct series, the innermost ones being composed of primary tissue. By a later growth of the central cylinder they become appressed to its periphery and flattened radially. This study brought to him and to his readers a conviction of the truth contained in his earlier suggestion that the cycads are closely related to the Medullosae, which are polystelic like the ferns. MATTE'S study of *Cycas siamensis* and *Encephalartos Barteri* (5) is an almost perfect demonstration of WORSDELL'S theory.

My work upon Ceratozamia will come as cumulative evidence. SOLMS'S statement concerning the absence of extrafascicular zones is correct as far as the seedling is concerned; but the presence of extrafascicular cambium in great abundance led me to make a careful search to discover its relation to the central cylinder. In the study of seedlings described in the previous paper I was unable to do this on account of the disturbances caused by mucilage ducts, which are large, abundant, and irregular in distribution. In the study of older stems I have been more fortunate. Four-year-old seedlings have in the hypocotyl clearly distinguishable rings or cylinders of cambium. The cylinders are arranged in several series. Those of the innermost series, though decidedly flattened, are the most distinct.

Fig. 1 represents diagrammatically a section of the hypocotyl slightly below the exit of the cotyledonary traces. The innermost cylinders (*a*, *b*, *s*) arise in the pericycle near the transition region and are of primary origin. They extend well up in the stem, though pushed outward by the horizontal cotyledonary traces. The other rings appear later. It would seem that the single bundle described in the previous paper (**3**, *fig. 30*, *z*) was differentiated from one of the outermost series of cylinders.

Fig. 2 is a detail of the inner portion of half the section represented in *fig. 1*. One large cambial ring (*a*) is represented, and ends of two others (*b* and *s*). Several small rings (*e*, *r*) suggest how concentric bundles might arise.

The cause of the flattening is manifestly the enlargement of the central cylinder and the consequent pressure upon the inner side of the cortical cylinders (*a*, *b*, *s*). The final result is a central cylinder surrounded by several more or less imperfect zones of cambium cells. The xylem and phloem which these cells might produce would be oriented differently; the xylem on the centripetal side of the zone would be differentiated toward the periphery and the phloem toward the center of the stem. But in many cases, the inner cambium of each zone would cease to function, and we should then have successive zones of alternating xylem and phloem all with normal orientation. Occasionally a bit of the elongated cylinder would be disconnected, the cambium would round out, the growth of xylem would eliminate the pith, and a concentric bundle would result. All these conditions are found in the Medullosae, from the distinct fern-like polystely in *Medullosa Solmsii* and *M. anglica* to the condition of *M. stellata*, which closely resembles *Cycas revoluta*.

I have not yet examined mature stems of plants of this genus. WORSDELL (**9**) has confirmed SOLMS-LAUBACH'S statement that the extrafas-

cicular zones are lacking; but MATTE (6) reports that he saw them in stems which he examined. I am therefore in doubt whether it is an absolute failure to function, or only a delay; in either case we have an indication that the cortical vascular tissue is a disappearing character.

Another feature to which attention should be called is the constant occurrence of centripetal xylem in the cylinder of the hypocotyl and in the bases of the cotyledonary bundles. This is represented in *fig. 28* of the paper already cited and also in *fig. 2* of the present one. It is often relatively more abundant than in some stems of Lyginodendron. The stem cylinder above the cotyledons is endarch, the leaf traces becoming mesarch almost immediately after leaving the cylinder.

Acknowledgments are due to Professor JOHN M. COULTER and Dr. W. J. G. LAND.—HELEN A. DORETY, *The University of Chicago.*

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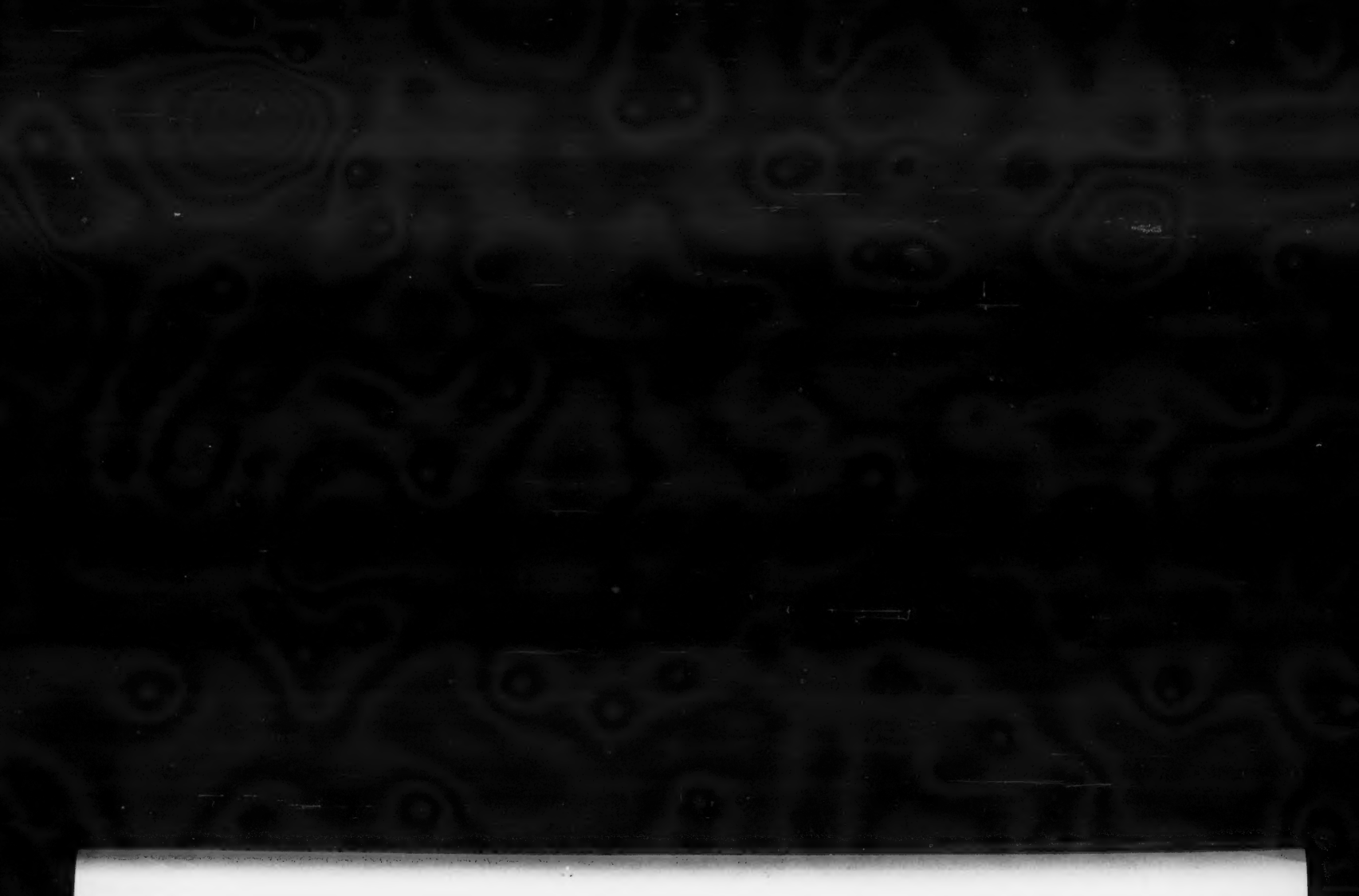

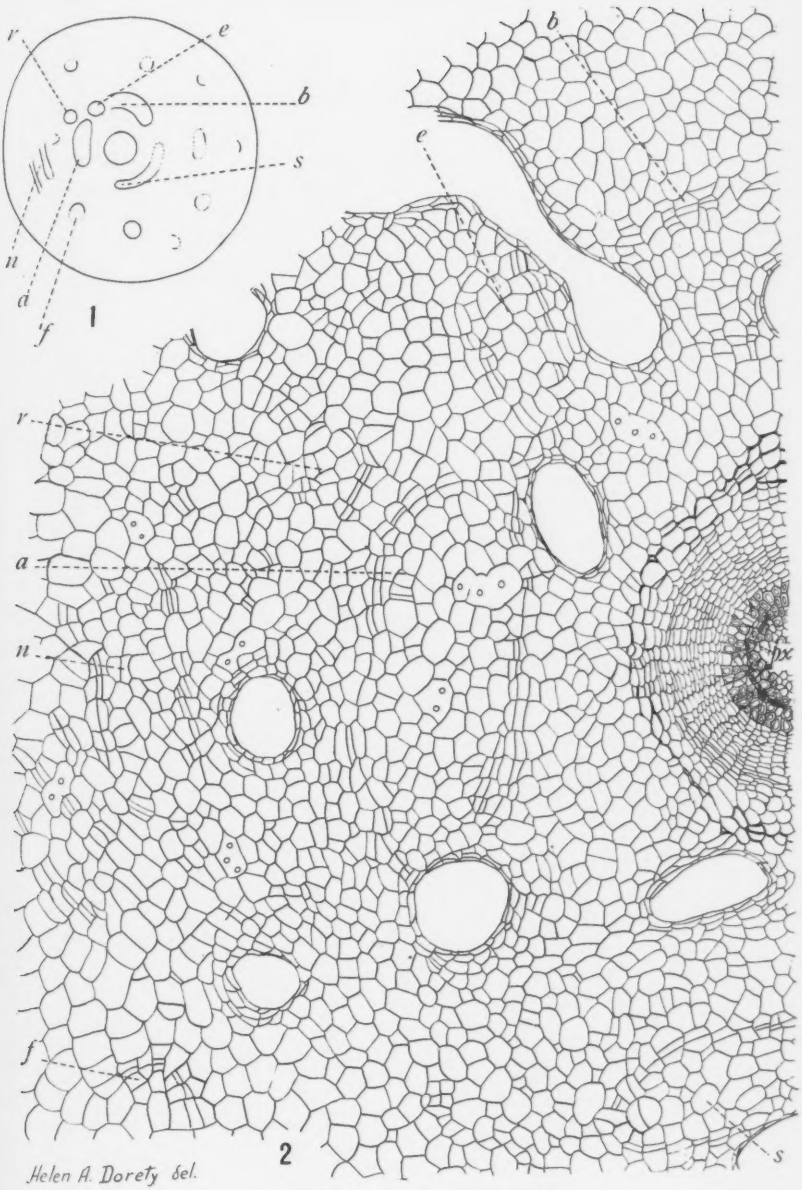

DORETY on CERATOZAMIA

CURRENT LITERATURE

BOOK REVIEWS

Gray's new manual of botany

It has been generally known for some time that GRAY'S *Manual* was undergoing a revision, so that the appearance of the seventh edition[1] was no surprise; in fact no book has been awaited by the botanical public, especially during the past three years, with so much interest as this one.

The present edition, contrasted with the sixth edition, presents the following more conspicuous changes: (1) a change in the geographical limits, namely by excluding the region west of the 96th meridian instead of the 100th, and in extending northeastward to include the maritime provinces and a portion of Quebec and Ontario; (2) the sequence of the families, which for the most part is in accordance with the system of EICHLER as elaborated by ENGLER and PRANTL; (3) the removal of the keys leading to the species, in the case of most of the larger genera, from the body of the text to a position immediately preceding the specific descriptions; (4) the introduction of numerous text- or marginal figures; and finally (5) in the use of a different system of nomenclature, namely the strict observance of the Vienna Code, or the nomenclatorial rules adopted at the International Congress held at Vienna in 1905.

The results of these innovations are that the flora treated is a somewhat more homogeneous one, the general arrangement and sequence of families is in accordance with advances made during recent years in the classification of plants, a greater facility and certainty in the identification of species by the use of direct keys and descriptions associated with accurately executed and reliable figures, and a greater consistency and uniformity in the use of plant names.

The general appearance of the printed page is essentially the same as in the sixth and in previous editions; the use of italics in emphasizing the more important specific characteristics is also retained. The treatment of genera and species is on the whole conservative and rational; and generic limitations are in close accord with general usage. The number of species is considerably larger than in previous editions, owing to the very active, careful, and exhaustive study of our flora during recent years.

The illustrations are judiciously distributed throughout the volume in groups where they are most useful, as, for example, in the Gramineae, Cyperaceae, Salicaceae, and Cruciferae; the Cyperaceae especially lend themselves to this type of illustration, and here they are certainly at their best. In some cases,

[1] ROBINSON, B. L., AND FERNALD, M. L., Gray's new manual of botany: a handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada. Seventh edition, illustrated, rearranged, and extensively revised. 8vo. pp. 926. *figs. 1036.* New York: American Book Co. 1908. $2.50.

for example in the Compositae, the illustrations have apparently suffered somewhat in the process of reproduction; thus for instance in the genus Crepis the illustrations, as reproduced, add little or nothing to the text. In general, however, the illustrations are excellent, and one only regrets that they are not more numerous.

The presswork is exceptionally good; there are few typographical errors. On page 500, however, "Abizzia" occurs instead of Albizzia, which is evidently a misprint.

The value of this work as a textbook should not be overlooked. The discriminating text and complementary illustrations present the subject-matter in a satisfactory way for teaching purposes. The illustrations themselves are for the most part insufficient for the hasty determination of the species by the student, and they can be used to advantage only in connection with the brief but clear descriptions. In this regard the book has no equal.

On the whole this new edition of the well-known GRAY'S *Manual* presents a flora of the central and northwestern United States, and adjacent Canada in a single volume of convenient size and moderate price, thoroughly revised to date, incorporating the verified results of recent years of research, and fully accords with the most advanced and universally accepted views of taxonomy.—J. M. GREENMAN.

Heredity

A recent volume on heredity, by PROFESSOR J. ARTHUR THOMSON[2] of the University of Aberdeen, "is intended," as the preface states, "as an introduction to the study of heredity." The writer has long been known as the joint author with GEDDES of the *Evolution of sex*, but is perhaps most widely recognized as the translator of WEISMANN'S works and the exponent of Weismannism. A review of such a book in a botanical journal needs no apology, for much of the more recent work in heredity has been done with plants, and moreover the book deals with those general fields of biological research which must always be of equal interest to botanists and zoologists. These fields will ever be the meeting-ground of botany and zoology, because in this class of problems the organism is treated as such, and the fact that it is a plant or an animal is of minor importance.

The work is divided into fourteen chapters, and among the topics dealt with may be mentioned the physical basis of inheritance; heredity and variation; reversion; telegony; transmission of acquired characters; statistical and experimental study of inheritance; theories of heredity and inheritance; heredity and sex; and a final chapter is devoted to the social aspects of biological results.

Heredity and inheritance are defined as follows (p. 13): "By 'heredity' we do not mean the general fact of observation that like tends to beget like, nor a power making for continuity or persistence of characters—to be opposed to the power of varying—nor anything but *the organic or genetic relation between succes-*

[2] THOMSON, J. ARTHUR, Heredity. pp. xvi+605. *figs. 49.* New York: G. P. Putnam's Sons. London: John Murray. 1908.

sive generations; and by 'inheritance' we mean 'organic inheritance'—all that the organism is or has to start with in virtue of its hereditary relation to parents and ancestors."

In the chapter on the physical basis of inheritance the author discusses the phenomena and experiments connected with chromosome reduction and fertilization, and concludes from the evidence that the chromosomes are the bearers of hereditary characters, but that "we should be chary in committing ourselves unreservedly to the conclusion that the heritable organization is *exclusively* resident in the chromatin of the nuclei of the germ cells." The chapter on heredity and variation contains a clear exposition of the facts and theories of mutation and continuous variation. The author believes that both are important evolutionary factors; that mutation, so far as present evidence goes, may have been a much more important factor in plants than with animals; and that the distinction between "large fluctuations" and "small mutations" is merely a verbal one. Regarding the causes of variation he considers it "useful to say that variation is the expression of a qualitative asymmetry beginning in gametogenesis." "Variation is a novel cell division."

There is a lengthy treatment of the question of the transmission of acquired characters or "somatic modifications;" with a critical analysis of the data usually cited as evidence. The result may be stated in the author's own words (p. 242): "The question resolves itself into a matter of fact. Have we any concrete evidence to warrant us believing that definite modifications are ever, as such or in any representative degree, transmitted? It appears to us that we have not. But to say dogmatically that such transmission is impossible is unscientific." The statistical studies of GALTON, PEARSON, and others are summarized, and under the experimental study of inheritance an array of data from the work of MENDEL, DEVRIES, BATESON, CORRENS, and many others of the recent school of genetics, which has begun to illuminate some of the obscure problems of hybridity, is brought together and discussed. These are largely the facts of Mendelism. In another part of the book blended, preponderant, and particulate inheritance are presented.

Other chapters are devoted to theories of heredity, which are largely theories of representative particles in some guise or other; and to theories of development, in which the author champions the determinants of WEISMANN and the latter's well-known theory of germinal selection. Under the topic heredity and sex, various theories of sex determination are discussed, including external and internal factors, and the author's theory is presented, namely that the difference in the sexes is merely a slight difference in "protoplasmic gearing" or in the "equation of metabolism." This view appears too vague to be of any value in directing the much-needed experiments on the subject. The author also apparently attaches too little significance to the discovery that in many insects an extra chromosome accompanies the female sex.

At the close of the work there is a representative bibliography of 48 pages, a very useful subject-index to the bibliography, and a general index to the volume.

The book is a broad and comprehensive treatment of the subject of heredity, a veritable mine of valuable data concisely presented and clearly discussed. The worker in these fields will find it almost indispensable for reference, and the more general reader will find it a very satisfactory and fascinating exposition of present-day views on these problems.—R. R. GATES.

Laboulbeniales

In 1896 the first part of a monograph of this group was published by THAXTER. The review in this journal[3] gave a general account of its contents, which presented the history, literature, and morphology of the group, in addition to the description of genera and species known at that time. During the last decade material has accumulated rapidly, and several preliminary papers describing it have been published. There has now appeared a second part of the monograph,[4] which brings together the material and illustrates it by a series of handsome plates. By means of visits to European collections and to South America, and through numerous correspondents, the new forms have multiplied remarkably. In the present part nearly 350 forms are illustrated, which increases the number described to about 500, included in more than 50 genera. In addition to these, more than 100 new species have been assembled since the completion of the present plates (in 1905), and these will be described and illustrated as soon as possible.

A brief review of the literature since 1895 is given, with comments on the morphology, development, etc., of the group, based upon the new data available. There is some modification in the conceptions of generic types, in the distinctions between series, etc.; but the comparative morphology of the group remains essentially as it was presented in 1895. This will be somewhat disappointing to those students of morphology who wish to relate Laboulbeniales positively to the Florideae; but the author wisely remarks that "it is foolish, on the basis of our present knowledge, to attempt an arbitrary settlement of the complex phenomena of series among the fungi." If he declines to be arbitrary about Laboulbeniales, no one else can afford to be so. Nevertheless, he thinks the statement safe that the group resembles the Florideae "in some respects more closely than they do any other plants, while at the same time they are more surely ascomycetes than many forms included in this group." He sees no reason why they should not be placed in the Pyrenomycetes, as a group coordinate with the Perisporiales, Hypocreales, etc.

This contribution, as the former one, is a model of painstaking and exact work, and of carefully weighed statement; and it is also an illustration of the wealth of material available for those who can see.—J. M. C.

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[3] BOT. GAZETTE **23**:216. 1897.

[4] THAXTER, ROLAND, Contribution toward a monograph of the Laboulbeniaceae. Part II. Mem. Amer. Acad. Sci. **13**:219–469. *pls. 28–61.* 1908.

African plants

Under the title *Die Blütenpflanzen Afrikas*,[5] Dr. FRANZ THONNER, after listing the chief botanical works and directing attention to some of the more scattered literature pertaining to the flora of Africa and supplying a detailed table of contents, gives a convenient key to the determination of the families of African flowering plants; then he presents the main body of the work, namely a key for the determination of the genera, which occupies about 540 pages. The text is supplemented by 150 plates, and a map indicating the floral regions and provinces of the continent.

Each family is described as to the essential and most striking characters and is represented, moreover, by a full page illustration of a characteristic genus; the number of genera and species of each family, so far as it occurs in Africa, is mentioned. Furthermore, the number of species in each genus and their geographical distribution is indicated.

The author presents no bibliography in connection with the text, and there is comparatively little in the way of synonomy; it is, however, definitely stated in the introduction that the limitations of families and genera are in accordance with ENGLER and PRANTL'S *Die natürlichen Pflanzenfamilien* and DALLA TORRE and HARMS'S *Genera Siphonogamarum*, so that for critical identification it will be necessary to use the book largely in connection with these and other important works of reference.

The keys are ingeniously arranged, well contrasted, and lucid; the illustrations are clear and advantageously portray the general and detailed characters of the plant, and well represent the different families. The volume also contains a carefully prepared comparative table giving the number of families, genera, and species as well as their general geographical distribution; it also contains a glossary, a list of botanical authors, and a useful catalogue of the common African plant-names associated with the proper scientific name.

On the whole the work brings together in an epitomized form and in a single volume much information concerning the flora of Africa that hitherto has been scattered through many different volumes; hence it is a work which will be of great practical use both in the herbarium and in the field.—J. M. GREENMAN.

MINOR NOTICES

Das Pflanzenreich.[6]—Part 36 consists of a monographic treatment of the Nepenthaceae by the well-known writer and authority on insectivorous plants, Professor J. M. MACFARLANE. An excellent general account of the family, following the usual sequence of this series, precedes the taxonomic consideration

[5] THONNER, FRANZ, Die Blütenpflanzen Afrikas: eine Anleitung zum Bestimmen der Gattungen der afrikanischen Siphonogamen. pp. xvi+673. *pls. 150. 1 map. M* 10 (12). Berlin: Friedländer & Sohn. 1908.

[6] ENGLER, A., Das Pflanzenreich. Heft 36 (iv. 111). Nepenthaceae von J. M. MACFARLANE. pp. 92. *figs. 19* (95). Leipzig: Wilhelm Engelmann. 1908. *M* 4.60.

of the group. A concise dichotomous key leads one direct to the species under which are numerous references to literature, synonomy, a detailed description, concise statement of geographical range, and a rather full citation of exsiccatae. The author recognizes 58 species and several varieties for the one genus Nepenthes, of which 8 species and 4 varieties are here published for the first time. The main body of the work is followed by an alphabetical list of artificial hybrids. These are designated by the binomial under which is given, so far as known, the names of parent species. The family is illustrated by 19 figures; a complete index concludes the part. The production is quite in accord with previous publications of this comprehensive and admirable series, and it is pleasing to note the tendency toward international cooperation which is already manifest in the *Pflanzenreich*.

Part 37, treating the Araceae[7] (begun in part 21 of this series), comprises: (1) a supplement to the Pothoideae in which a new genus (*Epipremnopsis*) is proposed with a single species, (2) an exhaustive treatise of the Monsteroideae, which reach their highest development in equatorial Asia and America, and in which group the authors recognize 12 genera and 190 species, 30 being new to science, and (3) an elaboration of the Calloideae with 4 monotypic genera. A concise key to the species precedes the larger genera, the species are clearly defined, and the numerous clean-cut illustrations happily combine general with essential detail characters.—J. M. GREENMAN.

Flora montana Formosae.[8]—This work concerns the mountain flora of the Island of Formosa, embracing the region lying at an elevation of 3000 to 13,000 feet. The total number of species recorded for this region is 392; the sebelong to 79 families and 266 genera. The author enumerates the various composing floral elements, such as the arctic, antarctic, alpine, tropical and North American, Malayan, Himalayan, southern, central, and northern Chinese, Japanese, and endemic. These upon summation show that "the flora is, in general, temperate, having as many as 320 species of temperate character, or 81 per cent. of the whole number of elements." The flora of the island has its strongest affinity with central and southern China and Japan, particularly as to the ratio of components, but as to their character "the flora of Formosa has as triking affinity to that of Japan." After a discussion of the general aspect of the vegetation and a division of the montane zone into four briefly characterized regions, the author follows with a detailed enumeration of the plants. In this list 69 species and 9 varieties are published as new to science. The descriptive matter is supple-

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[7] ENGLER, A., Das Pflanzenreich. Heft 37 (iv. 23 B). Additamentum ad Araceas-Pothoideas von A. ENGLER, Araceae-Monsteroideae von A. ENGLER UND K. KRAUSE, Araceae-Colloideae von K. KRAUSE. pp. 1–160. *figs 60* (*498*). *M* 8.40. Leipzig: Wilhelm Englemann. 1908.

[8] HAYATA, B., Flora montana Formosae. Jour. Sci. Coll. Tokyo **25**:1–260. *pls. 1–41*. 1908.

mented by several text-figures and carefully reproduced full-page illustrations. The work will serve as an excellent basis for future taxonomic investigation on the interesting flora of this island.—J. M. GREENMAN.

The United States as seen by de Vries.—Professor DE VRIES has published in the most attractive form an account of his experiences on his second American trip.[9] The volume is written in popular style, and is amply illustrated with unusually good half-tones depicting American scenery and universities. There are chapters on North Carolina with its cypress swamps and insectivorous plants; Arizona and the Grand Canyon; southern California with descriptions of San Diego, the marine vegetation of Santa Catalina, Pomona College, and a camping trip in the San Bernardino Mountains; the San Francisco earthquake, with special illustrations and descriptions of the disaster at Santa Rosa and Stanford University; the University of California, together with accounts of excursions to Mill Valley, Monterey, Mt. Hamilton, etc.; Great Salt Lake and Salt Lake City; agriculture in the central states, giving descriptions of the Kansas prairies, experiment stations and agricultural colleges in Kansas and Iowa, and maize culture in Illinois; and the dunes of Lake Michigan. One notices slight mistakes in the legends of two illustrations, a cut of Drosera being called Dionaea, and a scene among the University of Chicago buildings being attributed to the University of California. One in perusing this book longs for facility in the Dutch language, for the book contains the American impressions of one of the ablest men of our day. Botanists in these days too rarely write such volumes as this, perhaps because they feel that most of us are now globe-trotters, and able to be our own interpreters.—H. C. COWLES.

Algae and bryophytes of Connecticut.—The algae of the fresh waters of Connecticut have been described by Professor CONN and Mrs. WEBSTER in a preliminary report.[10] The descriptions and analytical keys and numerous drawings (from nature) bring these forms within easy reach of collectors and students.

The bryophytes of Connecticut have been described by Professor EVANS and Mr. NICHOLS.[11] An introduction (37 pp.) presents the general features of bryophytes, the history of their study in the state, their distribution according to environment, and their economic value. The catalogue, which includes keys and stations, makes the following enumeration: Marchantiales 12, Jungermanniales 92, Anthocerotales 3, Sphagnales 31, Andreaeales 2, Bryales 247, a total

[9] DE VRIES, HUGO, Naar Californië II. Haarlem: H. D. Tjeenk Willink & Zoon. 1907.

[10] CONN, H. W., AND WEBSTER, LUCIA W., A preliminary report on the algae of the fresh waters of Connecticut. pp. 78. *pls. 44 (figs. 291)*. Hartford: State Geol. and Nat. Hist. Survey, Bull. 10. 1908.

[11] EVANS, A. W., AND NICHOLS, G. E., The bryophytes of Connecticut. pp. 203. Hartford: State Geol. and Nat. Hist. Survey, Bull. 11. 1908.

of 387. Of these, 68 are peculiar to America, 244 are common to Europe and Asia, 61 are common to Europe but not to Asia, and 14 are common to Asia but not to Europe. The bibliography of "Connecticut bryology" contains 81 titles.—J. M. C.

British Basidiomycetes.—In 1905 the trustees of the British Museum secured the descriptions made by Mr. W. G. SMITH when preparing the series of colored drawings of British Fungi exhibited in the Department of Botany at South Kensington. Now these descriptions, accompanied by many line drawings illustrating generic characters, have been published as a handbook,[12] which it is hoped will be useful as an introduction to the field study of the fleshy fungi of Great Britain. A short introduction (8 pp.) gives a description of the general features and terminology of the group. The sequence followed is that of FRIES'S *Hymenomycetes Europaei* (1874), which is followed also in Great Britain by BERKELEY, COOKE, and STEVENSON. Space has been saved by reducing the descriptions of species to the salient distinctive characters, which must be supplemented by the generic and sectional characters. The total number of species presented is about 2130, distributed among 128 genera and 11 families. The Hymenomycetes include about 2050 of the species, 106 of the genera, and 6 of the families. A full glossary and a complete index conclude the volume, which should certainly stimulate the interest and activity hoped for.—J. M. C.

Tabulae Botanicae.—This excellent series of botanical charts, published by Gebrüder Borntraeger (Berlin), has been appearing during the last two years, and has proved to be of unusual value. They are larger than the ordinary charts, so that they can be seen well in a large lecture-room. Even more important is the fact that they are not current illustrations selected by one person, but they are in a sense original productions, each chart being designed by a specialist in the group presented, and executed by an artist under his supervision. Thus, BAUR has directed the illustrations of Myxobacteriaceae and Lichens, JAHN those of Myxomycetes, GUILLIERMOND those of the sexual forms of the yeasts, BLAKESLEE those of the mucors, etc. The charts have been raised slightly in price, being now *M*30 for a series of five unmounted. Dr. A. F. BLAKESLEE (Storrs, Conn.) has been asked to act as the American agent, and he will give information and transmit orders if desired.—J. M. C.

British Fungi.—In 1893 there was published a *Guide* to SOWERBY'S models of British Fungi, exhibited in the Department of Botany of the British Museum (Natural History). The purpose of the models was to exhibit to the public such a series of edible and poisonous species as would help to prevent the fatal mistakes often made from eating poisonous species. The work of restoring the

[12] SMITH, WORTHINGTON GEORGE, Synopsis of the British Basidiomycetes; a descriptive catalogue of the drawings and specimens in the Department of Botany, British Museum. 8vo. pp. 531. *pls. 5. figs. 145.* London: The Trustees of the British Museum. 1908. 10*s.*

fragile models was committed to Mr. WORTHINGTON G. SMITH, and in connection with this the *Guide* was published. There has now appeared[13] a second edition which has been carefully revised, and a glossary has been added.—J. M. C.

Natürlichen Pflanzenfamilien.—Parts 231, 232, and 233 continue the presentation of mosses by V. F. BROTHERUS, completing Thuidieae, and presenting Hypnaceae, Leucomiaceae, Sematophyllaceae, Rhegmatodontaceae, and Brachytheciaceae.—J. M. C.

NOTES FOR STUDENTS

Current taxonomic literature.—A. D. E. ELMER (Leaflets of Philippine Botany **1**:272–359. 1908) describes 100 new species of flowering plants, belonging to various genera, and (*idem* **2**:375–384) 9 new species of Lauraceae all indigenous to the Philippine Islands.—J. D. HOOKER (Hook. Ic. Pl. *pls. 2851–2875*. 1908) describes and illustrates 24 new species and one new variety of the genus Impatiens from China. The types are deposited either in the Paris, Le Mans, or Kew Herbarium.—V. L. KOMAROV (Acta Hort. Petrop. **29**:1–176. 1908), under the title of *Prolegomena ad floras Chinae nec non Mongoliae*, makes a valuable contribution to the literature concerning the flora of China; it includes, moreover, a critical revision of *Clematoclethra* Max., *Codonopsis* Wall., *Epimedium* and *Nitraria* L., in which genera 9 species and one variety are proposed as new to science.—HOMER D. HOUSE (Muhlenbergia **4**:49–56. 1908) gives a *Synopsis of the California species of Convolvulus*. The author recognizes 26 species, two of which are new.—W. P. HIERN (Journ. Bot. **46**:273–278. 1908) records the occurrence of a Sagittaria in the river Exe, near Exeter, England. The plant is described as a new variety of a North American species.—SPENCER LE M. MOORE (*idem* 290–298) describes 12 species of African plants as new to science, and proposes a new genus (*Grossweilera*) of Compositae; the same author (*idem* 305–313) characterizes 11 new species of African plants and a new genus (*Swynnertonia*) of the Asclepiadaceae, and also a new genus (*Eylesia*) of the Scrophulariaceae.—G. BONATI (Bull. Hb. Boiss. II. **8**:525–539. 1908) gives a synopsis of the genus Mazus. The author recognizes 24 species, 14 of which, and 2 varieties, are described as new.—J. BORNMÜLLER (*idem* 545–560) in a list of plants of the Elburz Mountains in northern Persia includes the description of a new species of Euphorbia.—FRANZ STEPHANI (*idem* 561–608, 661–696) describes 41 new species of Hepaticae, referred to various genera.—EDMOND MALINOWSKI (*idem* 623, 624) records a new species of Crucianella from Kurdistan.—HANS SCHINZ, in collaboration with different specialists (*idem* 625–640), describes 32 new species of African plants, including a new genus (*Pseudotragia*) of the Euphorbiaceae.—A. BRAND (Philip. Journ. Sci. **3**:1–10. 1908) gives a synopsis of the Symplocaceae of the Philippine Islands, in which 16 species are recognized, 6 of which, in addi-

[13] SMITH, WORTHINGTON GEORGE, Guide to SOWERBY'S models of British Fungi. Second edition, revised. pp. iv+85. *figs. 91*. London: The Trustees of the British Museum. 1908.

tion to 3 varieties, are described as new.—T. NAKAI (Journ. Coll. Sci. Imp. Univ. Tokyo **23**:1–28. 1908) presents a careful synopsis of the Polygonaceae of Corea and describes one new species and a new variety in the genus Polygonum.—N. L. BRITTON (Bull. Torr. Bot. Club **35**:337–345. 1908), under the title of *Studies of West Indian plants, I*, describes 5 species as new to science.—IG. URBAN, in collaboration with different specialists (Engl. Bot. Jahrb. **42**:49–176. 1908), under the title *Plantae novae andinae imprimis Weberbauerianae, IV*, has published 173 new species and 25 new varieties of South American plants, and also 4 new genera: *Fiebrigiella* (Leguminosae), *Centradeniastrum* (Melastomaceae), *Guraniopsis* (Cucurbitaceae), and *Huthia* (Polemoniaceae).—HENRI LECOMTE (Jour. Botanique II. **21**:101–109. 1908) describes 7 new species of Eriocaulon from Indo-China.—ALFRED CHABERT (Bull. Soc. Bot. France IV. **8**:305–310. *pls. 12, 13*. 1908) proposes 2 new varieties of *Campanula rhomboidalis* L. from France.—G. BONATI (*idem* 310–314) describes 4 new species of Pedicularis from China.—F. GAGNEPAIN (*idem* 322–325) describes 2 new species of the Capparidaceae from China.—E. A. FINET (*idem* 333–343) has published 11 new species and 1 variety of orchidaceous plants from South America and from different parts of the Old World.—H. LÉVEILLÉ (*idem* 407–409) recognizes 5 species of Mucuna indigenous to China, 2 of which are described as new.—S. T. DUNN (Jour. Linn. Soc. London **38**:350–373. 1908) gives an account of *A botanical expedition to Fokien, China*, followed by descriptions of 37 new species and 1 new variety.—T. F. CHIPP (*idem* 374–391) in *A revision of the genus Codonopsis* recognizes 22 species, 4 of which are new to science.—Various authors, under the title *Diagnoses Africanae, XXIV* (Kew Bull. pp. 286–300. 1908), have published 16 new species and 5 varieties of African plants, including a new genus (*Cotylonychia*) of the Sterculiaceae, and also a new genus (*Hemandradenia*) of the Connaraceae.—HENRY PITTIER (Contrib. U. S. Nat. Herb. **12**:159–169. 1908), following a general discussion of the genus *Sapium* and an analytical key to the Mexican and Central American species, describes and illustrates the 9 species recognized for this region; of these 6 are new to science, and 4 are published in joint authorship with the late Prof. KARL SCHUMANN.—ED. PALLA (Oesterr. Bot. Zeitschr. **58**:389–392. 1908) describes 3 new species of Cyperaceae from Mexico and Colombia.—CHARLES BROOKS (Bull. Torr. Bot. Club **35**:423–456. 1908) gives an account of *The fruit spot of apples* and records a new species of the genus Cylindrosporium.—P. A. RYDBERG (*idem* 457–465) recognizes 6 species of Philotria for this country, one being described as new.—EUGENE P. BICKNELL (*idem* 471–498), under the title *Ferns and flowering plants of Nantucket, III*, has published 2 new species and proposes 7 new combinations chiefly in the genus Carex.—FRANK D. KERN (*idem* 499–511) in *Studies in the genus Gymnosporangium* publishes 3 new species and makes 3 new combinations.—F. PETRAK (Fedde, Rep. Nov. Sp. **5**:329–333. 1908) describes 9 new hybrids and 1 new variety in the genus Cirsium from southern Europe.—E. HACKEL (*idem* 333–335) records a new species of Phalaris from Australia.—F. KRÄNZLEIN (*idem* 369, 370) has described a new species of Calceolaria from Bolivia.—E. ROSENSTOCK (*idem* 370–376) has published 6 new

species and 5 varieties of ferns from New Guinea.—J. BORNMÜLLER (*idem* 376, 377) records a new species of Reaumuria from Persia.—D. GRIFFITHS (Rep. Mo. Bot. Gard. **19**:259–272. *pls. 21–28.* 1908), under the title *Illustrated studies in the genus Opuntia—I*, has described 15 new species of Opuntia from Mexico and the southwest.—W. GUGLER (Ann. Mus. Hung. **6**:15–297. *pl. 1.* 1908), under the title of *Die Centaureen des Ungarischen National-Museums*, records in detail the species and subordinate categories of the genus Centaurea represented in the Hungarian National Museum; the work is preliminary to a monograph of this genus.—F. STEPHANI (Bull. Herb. Boiss. II. **8**:837–866. 1908) has described 45 new species of Hepaticae, of which several are American.—B. DE LESDAIN (Bull. Soc. Bot. France IV. **8**:420–424. 1908), under *Notes lichénologiques*, describes 3 species and 2 varieties as new to science.—H. LÉVEILLÉ (*idem* 424–427) enumerates 11 species of the genus Pueraria for China, of which 5 are published in joint authorship with VAUT.—P. DOP (*idem* 427–430) describes 3 new species of the Malpighiaceae from Indo-China.—F. GAGNEPAIN (*idem* 430–436) proposes 3 new species of the Zingiberaceae from Oceania.—H. DE BOISSIEU (*idem* 467–470) has described 4 species and 3 varieties of Violaceae from the Orient.—L. A. DONDE (*idem* 470, 471) has published a new species of Carya from Mexico.—H. COSTE (*idem* 472–476) records 2 new hybrids in the genus Cistus from southern France.—A. W. EVANS (Rhodora **10**:185–193. 1908) publishes further notes concerning New England Hepaticae. The total number of species in this group thus far recorded for New England is 147.—A. DAVIDSON (Muhlenbergia **4**:65–68. 1908) lists a collection of plants made in the Tehachapi Mountains, California, and proposes a new species in the genus Fritillaria.—D. PRAIN (Bull. Kew 381–387. 1908) gives a short history of Butea, a brief revision of the genus, and records 1 new species.—N. E. BROWN and O. STAPF (*idem* 407–412) describe 10 new species of African plants.—R. A. ROLFE (*idem* 412–416), under the title of *New orchids: Decade 32*, has published 10 new species.—T. F. CHEESEMAN (*idem* 419–421) records a new species of the genus Bagnisia from New Zealand.—E. DE WILDEMAN (Pl. Fl. Congo **2**:167–268. 1908), in connection with certain economic studies, has published 7 new species and 2 new varieties of Apocynaceous plants of Africa, chiefly from the Congo region.—B. SCHROEDER (Ber. Deutsch. Bot. Gesells. **26a**:615–620. 1908) has published 2 new species of Bacillariaceae from plankton of the Adriatic Sea.—J. H. MAIDEN and E. BETCHE (Proc. Linn. Soc. N. S. W. **33**:304–319. 1908) have published 5 new species and 3 new varieties of Australian flowering plants.—G. E. MATTEI (Boll. R. Orto Bot. Giard. Col. Palermo **7**:85–112. 1908), under the title *Contribuzioni alla Flora della Somalia italiana*, has described 9 new species of flowering plants.—C. S. SARGENT (Ont. Nat. Sci. Bull. 11–98. 1908) has described 44 new species of Crataegus from Ontario: the same author (Rep. Mo. Bot. Gard. **19**:35–126. 1908) proposes 69 new species of Crataegus from Missouri, and in another place (Bull. N. Y. State Mus. 122:26–130. 1908) 83 from New York.—C. H. PECK (*idem* 5–25, 131–160) has published 8 new species of fungi from New York.—H. CHRIST (Philip. Journ. Sci. **3**:269–276. 1908) has published 12 new species

and 2 new varieties of Philippine ferns.—E. B. COPELAND (*idem* 277–284) describes 8 new species and 3 new varieties of ferns from China; and the same author (*idem* 285–300) presents *A revision of the Philippine species of Athyrium* in which 46 species are recognized, 5 species and 1 variety being described as new to science. —E. D. MERRILL (*idem* 307–315), under the title of *Philippine Freycinetia*, records 24 species of this genus from the Philippine Islands, 8 being described as new; and the same author (*idem* 317–338) has published 6 new species of oaks and 6 new species and 1 new variety of the genus Radermachera from the Philippine Islands. —R. WAGNER (Oesterr. Bot. Zeits. **58**:435–439. 1908) has described a new species of Tropaeolum from Columbia.—F. SENNEN (Bull. Acad. Intern. Geogr. Bot. III. **17**:449–480. 1908), under the title of *Plantes d'Espagne*, has published in joint authorship with C. PAU 6 new species and several new varieties of flowering plants from Spain.—R. FRIES (K. Sv. Vet. Akad. Handl. **42**:1–67. *pls. 1–7*. 1908) has published 23 new species and 14 new varieties of Malvales, chiefly from South America; the same author (*idem* **43**:1–114. *pls. 1–10*. 1908) recognizes 37 species for the genus Wissadula, of which 11 species and 4 varieties are described as new, and a new genus (*Pseudoabutilon*) of the Malvaceae is proposed, to which are referred 9 species, 3 being new to science.—K. JOHANSSON (Arkiv för Botanik **7**:no. 12, pp. 48. *pls. 1–5*. 1908), under the title *Hieracia vulgata Fr. från Torne Lappmark*, enumerates 35 species, 20 of which and 3 varieties are described as new.—J. M. GREENMAN.

Effect of light on germination of seeds.—HEINRICHER[14] has recently added two more papers to his series on the effect of light on germination, and KINZEL[15] publishes a second paper (preliminary statement) on his extensive researches on this subject. Data enough are now at hand to get at some general principles. In respect to the effect of white light upon their germination, seeds may be divided into four groups: those requiring light for germination (*Rhododendron javanicum*, *R. hirsutum*, *R. ferrugineum*, *Drosera capensis*, etc.); those germinating more quickly and fully in light (*Veronica peregrina*, *Allium suaveolens*, etc.); those germinating equally well in light and darkness (*Myrmecodia echinata*, etc.); and those retarded in germination by light (*Phacelia tanacetifolia*, *Pedicularis Sceptrum Carolinium*). It is agreed by both authors that the favorable effect of light is not due to its causing an early carbon assimilation, but rather to its effect upon enzyme activity on production and therefore upon the digestion of stored foods. The conclusion concerning photosynthesis seems to be justified, for in all cases tested the light is as effective in CO_2-free chambers as in chambers containing CO_2. The effects of different rays as stated in the following paragraph also seem

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[14] HEINRICHER, E., (1) Beeinflüssung der Samenkeimung durch das Licht. Wiesner-Festschrift. Wien. 1908. (2) Die Samenkeimung und das Licht. Ber. Deutsch. Bot. Gesells. **26a**:298–301. 1908.

[15] KINZEL, W., Die Wirkung des Lichtes auf die Keimung. Ber. Deutsch. Bot. Gesells. **26a**:105–115. *figs. 4*. 1908.

to support this conclusion. I see no grounds, however, for concluding that the effect is upon the digestive enzymes rather than upon some other mechanism of the protoplasm.

KINZEL's attention has been largely centered upon the effects of rays of different refrangibility. HEINRICHER[16] early found that the red end of the spectrum was most effective in *Veronica peregrina*. KINZEL's results indicate that this is generally the case. Among different species, however, there is a great variation in the relative effectiveness of various rays. Green is by far the most effective with Nicotiana, while with Veronica yellow gives the greatest stimulation. KINZEL finds the blue rays least effective; in fact they often cause marked retardation. In many cases of seeds favored in germination by light, blue gave a much slower and lower percentage of germination than darkness. KINZEL comments upon the general retarding effect of blue light, while HEINRICHER later points out that in the seeds of *Phacelia tanacetifolia* which are retarded in germination by white light, blue markedly stimulates germination.

Many of the "light-loving" seeds demand a considerable period of rest after harvest, during which they become thoroughly dried out. In *Veronica bellidioides* three and one-half months was the most effective period. In the short-lived seeds of Drosera fifteen hours of drying in the laboratory best effected their "after-ripening." HEINRICHER says, "On the whole the experiments indicate that the results in the germination of such seeds as are helped by light depends upon the age of the seed, upon the quickness of drying after harvest, further, also, upon whether this takes place in light or darkness, and, if in the first way, whether in one layer or several. Finally, even the moisture content of the air during storage must be considered as a factor. It is evident that the conditions are extraordinarily complex and that conformity of results is to be expected only under the consideration of all these factors."

HEINRICHER believes that the similarity in behavior of various seeds toward light is more often connected with their phyletic relationships than with likeness of ecological habit.

It seems to the reviewer that in cases where evident coats appear, the investigators should work with coat-free seeds to make sure that the coats by partial exclusion of oxygen, salts, or even water are not hindering germination. In such cases light may be a means of compensating some other limiting condition of germination. It is also evident, from the variable results, that the real solution of the problem will come from learning the particular dormant process in each case that is aroused by light. This ought to be possible in view of the great advance being made in our knowledge of the catalytic nature of protoplasmic activity, but it will demand an attack on the problem from other points than the mere effects of light upon the living seeds.—WM. CROCKER.

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[16] HEINRICHER, E., Ein Fall beschleunigendes Wirkung. Ber. Deutsch. Bot. Gesells. **17**:308–311. 1899.

Observations on Welwitschia.—PEARSON has communicated further studies on this peculiar genus to the Royal Society, London, of which the following is an abstract.

Macrospores and embryo sacs are frequently present in the pith region of the female cone-axis. This confirms the view, already adopted by most authors, that the ovule of Welwitschia is cauline. Sporogenous cells have not been found in a similar position in the male cone.

It is suggested that the female cone and the male flower are derived by reduction and specialization from an amphisporangiate strobilus of a type similar to that of Bennettites.

At the end of the free nuclear division the embryo sac contains about 1024 nuclei which are equivalent in all visible characters. Cleavage of the cytoplasm occurs, resulting in the septation of the whole sac into compartments. Those near the micropylar end contain few nuclei which are functionally sexual; most of those of the lower three-fourths inclose many potentially sexual nuclei. The former send out embryo-sac tubes into the nucellar cone and into them pass the cytoplasm and free nuclei; all the nuclei in each of the latter fuse so that each compartment becomes a uninucleate cell. The compartments containing the fusion nuclei form the primary endosperm, whose later growth is distributed over two periods, one before and the second after fertilization. The endosperm of Gnetum is probably formed in the same way. In respect of the morphological character of the endosperm, Gnetum and Welwitschia are widely separated from Ephedra, in which the endosperm is a prothallus of the normal gymnosperm type. It is suggested that the endosperm of the primitive angiosperms was homologous with that of Welwitschia.

The embryo-sac tubes meet the pollen tubes in the lower half of the nucellar cone. Fertilization occurs within the generative cell, which enlarges after leaving the pollen grain and its nucleus divides. The daughter nuclei are functional gametes.

Several oospores are commonly formed in each nucellus. The cytoplasm of the oospore is mainly, if not entirely, provided by the generative cell. A resting nucleus is formed. The oospore elongates toward the top of the endosperm. The first nuclear division within it is followed by the formation of a centripetally developed wall which separates the upper "primary suspensor" from a lower terminal cell. From the latter are developed: (*a*) 24 cells which, surrounding the lower part of the primary suspensor, form with it "the secondary suspensor;" (*b*) a terminal group inclosing a presumed embryonic plate of eight cells. The later stages of embryo development have not been seen; they possibly occur, as in Gnetum, after the seed is detached from the plant.

It is suggested that (1) the Gnetum-Welwitschia alliance has its origin in the same stock as the angiosperms, but separated from the angiosperm line before the carpel became the pollen-receiver; (2) Welwitschia is the most specialized living representative of the race to which it belongs.

Mucilage ducts in Pipereae.—In considering the genera of the Piperaceae, two tribes are recognized by VAN TIEGHEM,[17] namely Pipereae and Peperomieae; while the Saururaceae are kept as a distinct family, as suggested a hundred years ago by L. CL. RICHARD. By CASIMIR DECANDOLLE the Saururaceae were replaced in Piperaceae as a tribe; and then separated by ENGLER. In speaking of Piperaceae, therefore, VAN TIEGHEM does not include Saururus and its allies. From an anatomical point of view the Piperaceae have long attracted much attention, especially on account of peculiarities in stem structure, which at the same time are characteristic of the respective tribes. For instance, in the Pipereae the stem exhibits a normal monostelic structure, with the broad stele surrounded by a well-differentiated endodermis, and possesses at least two concentric bands of mestome bundles. In the Peperomieae, on the other hand, the stem structure is of the schizostelic type, the numerous meristeles being scattered, not arranged in bands, and each being provided with a special endodermis. Common to both tribes, however, is the presence of roundish oil cells with the cell wall suberized or at times lignified; these oil cells are widely distributed through stem and leaf. In certain Pipereae still another secreting system occurs, which is now for the first time described. It consists of a single duct or several broad ducts containing mucilage and extending through the full length of stem and leaf; these ducts are lysigenous, since they arise from the destruction of a row of secreting cells. They occur in the pith of the stem, mostly a very broad one in the center and several narrower ones in a band around this and alternating with the innermost mestome strands. They contain a colorless mucilage, and are surrounded by small cells, notably smaller than those of the surrounding pith parenchyma. This system of secretory ducts belonging to the stem stele is readily followed through the internodes, but disappears completely in the nodes. In the leaf these ducts occur in the petiole, in the parenchyma located on the ventral (the hadromatic) face of the arch formed by the mestome strands; thence they may be traced in the midrib of the leaf blade, from the base to apex. Although the author examined various representatives of the Peperomieae, he failed to detect the ducts in any of them. Among the Pipereae they occur in Piper (as in *P. nigrum*, *P. Cubeba*, *P. macrophyllum*, etc.), in *Chavica Blumei*, *C. sphaerostachya*, and some species of Heckeria; while they are not developed in Macropiper, Nematanthera, and Zippelia.—THEO. HOLM.

Studies in aquatic plants.—FRANÇOIS[18] has offered a very interesting contribution to the knowledge of aquatic plants with notes on their structure, external as well as internal, and on their seedlings, the text containing many well-drawn figures. Special attention is given to the vegetative reproduction of such

[17] VAN TIEGHEM, PH., Sur les canaux à mucilage des Piperées. Ann. Sci. Nat. Bot. IX. 7:117. 1908.

[18] FRANÇOIS, L., Recherches sur les plantes aquatiques. Ann. Sci. Nat. Bot. IX. 7:25. 1908.

species as occur on river banks, the stolons of which grow in the water, creeping over the muddy bottom. Among these are *Mentha aquatica*, *Lysimachia vulgaris*, *Lycopus europaeus*, *Stachys palustris*, partly also *Potentilla reptans*, *Ranunculus repens*, and *Cynodon Dactylon*. In these the vegetative reproduction is amply secured by the ability of the fragments of the rhizomes and stolons to root very easily, and at the same time the water currents help to disperse such fragments over wide areas. The seedling stage of Butomus, various species of Alisma, Sagittaria, Najas, and Potamogeton is described. The slow growth of the primary root is characteristic, while the hypocotyl attains its final length in a very short time, and before the root actually commences its increase in length. The primary root stele in Butomus and in Alismaceae consists of a single central vessel and of two strands of leptome diametrically opposite each other. In the Najadaceae, on the other hand, several vessels are developed, the largest of which is usually located in or near the center, and there are also several strands of leptome, corresponding in number with the rays of hadrome. The hypocotyl exhibits a bilateral structure in Butomus and Alisma and no pericycle was observed inside the endodermis. In the Najadaceae the bilateral structure is much less pronounced, and no stomata were observed in the epidermis of the hypocotyl of any of these plants. A very simple structure characterizes the cotyledon; the chlorenchyma is homogeneous and contains only one vein near the ventral face. The seedling stages are very carefully described and figured, adding several interesting points to the knowledge of the structure of aquatic plants.—THEO. HOLM.

Organic correlations.—EAST[19] attempts a classification of correlations with especial consideration of plant data. This is a little-known field at the present time, but one of great promise for the future. The writer of course realizes that this tentative classification awaits the accumulation of further data to place it on any satisfactory basis. Correlations are considered as "somatic" and "gametic." Under somatic correlations are classed: (1) correlated reactions to environment; here are placed the experimental results of MACDOUGAL in Raimannia and of TOWER in Leptinotarsa, although the indications are that these changes are germinal and not somatic; (2) growth correlations between (*a*) non-homologous, (*b*) homologous, and (*c*) meristic parts; (3) correlations in organs of a plant; (4) interdependent and exclusive development; here is cited the case of *Oenothera lata*, in which the broad-leaved character is associated with the "inability to produce healthy pollen;" but this association is not constant, for plants from England having the *O. lata* characters have been successfully self-pollinated;[20]

[19] EAST, EDWARD M., Organic correlations. Amer. Breeders' Assoc. **4**:pp. 12. 1908.

[20] MACDOUGAL, D. T., VAIL, A. M., AND SHULL, G. H., Mutations, variations, and relationships of the Oenotheras. Carnegie Inst. Publ. **81**:pp. 92. 1907; and unpublished results of the reviewer.

(5) heterozygotes; in the numerous cases where heterozygotes differ from either parent, "the ability to transmit certain characters is correlated with other *apparent* characters." Under gametic correlations are placed the phenomena of partial and complete "coupling," so called, developed chiefly by BATESON.—R. R. GATES.

Tyloses in ferns.—It has been noted by various writers that in the stems and petioles of ferns the protoxylem groups suffer disintegration, and into the cavities so formed the wood-parenchyma grows, forming the "cavity-parenchyma" of Russow. Proliferations from these cells frequently fill the cavities, and present the appearance of tyloses. These growths have recently been studied in detail by two independent workers, KIRSCH[21] and Miss MCNICHOL.[22] Both writers show that the phenomenon is widespread, being found in nearly every family of the true ferns, as well as in Marsilia and the Ophioglossaceae. In both papers the cells in question are carefully described and their origin as stated above is proven. KIRSCH has studied *Pteris aquilina* in most detail, and finds cavity-parenchyma in the stipe and in all regions of the rhizome, where it occurs in the outer system of bundles which he erroneously regards as cortical (p. 388). He offers the following as a theory of the cause of these growths: the cavity formed by disintegration of the protoxylem at first functions as a water duct; later the metaxylem (secondary xylem according to KIRSCH) makes its appearance and performs the duty of water carrier. Hence the pressure in the cavity is reduced, and as a consequence tyloses grow into it.—M. A. CHRYSLER.

Composition of a field of maize.—A brief paper by SHULL[23] calls attention to the view, already expressed by DEVRIES and others, that a field of corn, like wheat and other grains, is made up of a number of elementary species or biotypes. He discusses the fact that inbreeding in corn results in deterioration, and points out that the old hypothesis that the deleterious effects of inbreeding result from the accumulation of disadvantageous individual variations to form an organism with an inharmonious or unbalanced constitution, is untenable, in view of the facts of cleistogamy, self-pollination, and parthenogenesis in plants which have evidently been successful in the struggle for existence. A cornfield is conceived to be a series of hybrids between elementary species, and on the basis of the common observation that hybrids between nearly related forms are more vigorous than either parent, he believes that over-selection, which eliminates down to a single biotype, results in deterioration, not intrinsically from inbreeding, but because the greater vigor which comes from the crossing of biotypes has been eliminated. The

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[21] KIRSCH, SIMON, On the development and function of certain structures in the stipe and rhizome of *Pteris aquilina* and other Pteridophytes. Trans. Royal Soc. Canada III. **1**[4]:353–412. *figs. 27+21.* 1907.

[22] MCNICHOL, M., On cavity parenchyma and tyloses in ferns. Annals of Botany **22**:401–413. *pl. 25.* 1908.

[23] SHULL, GEO. H., The composition of a field of maize. Amer. Breeders' Assoc. **4**:pp. 6. 1908.

ideal of the corn-breeder should then be continuous hybridization between biotypes, rather than the isolation of pure strains.—R. R. GATES.

Isolation and mutation.—While the final adjudication of the claims of the various theories of evolution must be made on an experimental basis, such data must be in harmony with the facts of plant and animal distribution, as is pointed out in a suggestive paper by LEAVITT.[24] It is of much interest to observe that zoologists, as a rule, have been less inclined to believe in mutation than have botanists. This is in part due, LEAVITT thinks, to a less perfect grasp of the theory by some of the zoologists, but in part due also to the fact that most students of animal distribution believe that isolation of closely related species is a most important principle in evolution. The author shows that there are innumerable cases of overlap in closely related plants of all groups, most notable, perhaps, in the widely varying thallophytes and bryophytes, but abundant in the seed plants. There is plenty of evidence that new species may have originated from the old without geographic isolation, although cases suggesting the latter are not wanting. Therefore, it is concluded, many facts of plant distribution favor the mutation theory, though they do not show that this is the only valid theory of evolution.—H. C. COWLES.

Osmotic properties of root hairs.—HILL[25] has investigated the osmotic properties of the root hairs of *Glyceria maritima*, *Suaeda maritima*, and *Salicornia herbacea*, which grow in a salt marsh subject to great changes in the osmotic pressure of its soil water, due to periodic flooding by the tides and to occasional drenching rains. He finds that the hairs show marked and rather rapid variation in osmotic pressure corresponding in variation to the osmotic pressure of the soil water. This variation is not due to the entrance of the abundant chlorids of the soil water, for in no case could he find chlorids in the root hairs, although they could be found in traces in the upper portions of the seedlings. The high osmotic pressure of the soil water seems to act through the irritability of the protoplasm, causing a dissociation of the compounds of the cells. He thinks OSTERHOUT is wrong in concluding that osmosis is not an important process in plant nutrition, and points out the fact that all the data of this investigator can be explained by the fact that plants can modify their osmotic properties readily in response to and in protection against rapidly varying external osmotic pressures.—WILLIAM CROCKER.

Statolith theory.—BUDER[26] comes to the support of the statolith theory with a set of well-chosen and critical experiments that seem to justify his conclusions,

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[24] LEAVITT, R. S., The geographic distribution of nearly related species. Amer. Nat. **41**:207–240. 1907.

[25] HILL, F. G., Observations on the osmotic properties of the root hairs of certain salt marsh plants. New Phytologist **7**:133–142. 1908.

[26] BUDER, JOHANNES, Untersuchungen zur Statolithenhypothese. Festschrift zur Feier des 25-jährigen Bestehens der Deutsch. Bot. Gesells. Ber. **26**:162–193. 1908.

which are briefly as follows: Contrary to FITTING's conclusion, in a combination of the rest position with various angles, the statolith starch takes the position that would be expected by the statolith theory. Centrifugal acceleration causes the movement of the starch that the hypothesis assumes, as shown by accelerations from 0.13 *g* to 9 *g*. In these various accelerations the time of the movement of the starch to the side of the cells coincides with the presentation time as determined by BACH. In the intermittent exposures of opposite sides when these exposures are of short duration the starch moves to the side of the cell of the most effective exposure only after the process is long continued, corresponding to the slow reaction in these cases. However well this paper may answer a number of the arguments against the statolith theory, there are yet a number unanswered and this whole matter of geotropic reaction seems too complex to be entirely explained in such a simple way.—WM. CROCKER.

Ray-tracheids in Cunninghamia.—The complex structure of the medullary rays of living Abietineae, consisting of parenchyma cells, ray-tracheids, and an elaborate system of ligneous resin-canals, has been used as one of the evidences of a highly specialized and relatively modern group. JEFFREY[27] has studied the marginal ray-tracheids that occur occasionally in Cunninghamia and has found them to be due to wounding, being most numerous in the region of the injured annual rings opposits the wound-callus. They resemble in general those described for certain genera of the Taxodineae and Cupressineae, and JEFFREY thinks that this is additional evidence that these two tribes have been derived from the Abietineae, the ray-tracheids being "vestigial or reversionary." He emphasizes this view by calling attention to the fact that there is no evidence that the Taxodineae and Cupressineae existed before the end of the Cretaceous. Such conclusions illustrate the fact that apparent simplicity of structure may not indicate greater antiquity than greater complexity of structure.—J. M. C.

Vascular system of Ranales.—WORSDELL[28] maintains that the primitive angiosperms had large leaves, and that as a result the vascular bundles were disposed in a scattered manner, as is seen in the monocotyledons. He considers that there is in all cases a single terminal cotyledon in the embryo, but that it may split and the halves diverge through 180°. Like the cotyledon, all the leaves are terminal organs, and hence dominate the stem ("grandifoliate"). From this condition has been derived the one in which the stem is dominant and the leaves small ("parvifoliate"). This view of phylogeny naturally leads WORSDELL to reject the evidence derived from the vascular system of seedlings adduced by JEFFREY and others, although he claims to adopt the "recapitulation theory." In the present paper he outlines the results of an extensive study of the leaves in

[27] JEFFREY, EDWARD C., Traumatic ray-tracheids in *Cunninghamia sinensis*. Annals of Botany **22**:593–602. *pl. 31*. 1908.

[28] WORSDELL, W. C., A study of the vascular system in certain orders of the Ranales. Annals of Botany **22**:651–682. *pls. 32, 33*. 1908.

certain representatives of Ranales, and shows how the scattered bundles of a petiole may be converted into a ring, and the bundles of one side of the ring approximate the opposite side so as to produce a single arc.—M. A. CHRYSLER.

Solution of mitoses.—Experiments of OES[29] with various root tips, embryo sacs, and pollen mother cells show that cells capable of growth and division contain a chromatin-dissolving enzyme (*nuclease*), which dissolves chromatin when toluol, chloroform, carbolic acid, etc., are added. Metaphases, anaphases, and telophase are most quickly attacked, the prophases being less susceptible, and the resting nucleus still more resistant. In autolyzed objects the spindle is dissolved, but the nucleolus and nuclear membrane of resting nuclei remain unaffected. The effect of temperature, neutral salts, free acids, and alkalies was observed in various objects. The writer believes that the diminution of chromatin in the telophase, observed by STRASBURGER and others, may be due to nuclease. If nuclease functions in the normal, living plant, thus causing irregular fluctuations in the chromatin, the question arises whether chromatin is the exclusive bearer of hereditary qualities.—CHARLES J. CHAMBERLAIN.

Tyloses in tracheids of Conifers.—CHRYSLER[30] has reinvestigated this subject, and finds tyloses in the heart wood of the root, and in the first year's growth of the axis of the strobilus. So far as his work goes, they are confined to Pinus, the examination of the root wood of 12 other genera and of the cone axes of 7 other genera failing to reveal them. The effect of wounding was also studied, but it did not result in extending the range of tyloses, either to other genera or to other regions of Pinus; but wounding did result in inducing the occurrence of tyloses in the normal regions of Pinus. It is suggested that these facts may provide an additional reason for considering Pinus to be an ancient genus.—J. M. C.

Plant diseases.—STEWART and HODGKISS in a recent bulletin[31] discuss the carnation bud rot previously described by HEALD and WOLCOTT of the Nebraska Experiment Station. It is a disease which is known to occur in New York, Illinois, and Nebraska, and which is attributed to a species Sporotrichum with the association of a species of mite.

The disease of grass known as silver top is also discussed in this same bulletin and attributed to the same fungus in association with the same mite, though the relation of the mite to infection has not been completely worked out in either case.—F. L. STEVENS.

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[29] OES, ADOLF, Ueber die Autolysis der Mitosen. Bot. Zeit. **66**:89–120. *pl.* 5. 1908.

[30] CHRYSLER, M. A., Tyloses in tracheids of Conifers. New Phytol. **7**:198–204. *pl.* 5. 1908.

[31] STEWART, F. C., AND HODGKISS, H. E., Tech. Bull. 7, N. Y. Agric. Exper. Sta. Oct. 19, 1908.